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The Wilson Bulletin

PUBLISHED BY THE WILSON ORNITHOLOGICAL SOCIETY

VOLUME 87 1975 QUARTERLY

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DATES OF ISSUE OF VOLUME 87
OF THE WILSON BULLETIN

NO. 1—26 MARCH 1975
NO. 2—30 MAY 1975
NO. 3—29 SEPTEMBER 1975
NO. 4— 8 JANUARY 1976

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The Wilson Bulletin

PUBLISHED BY THE WILSON ORNITHOLOGICAL SOCIETY

VOL. 87, NO. 1 MARCH 1975 PAGES 1–144

THE WILSON ORNITHOLOGICAL SOCIETY

FOUNDED DECEMBER 3, 1888

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THE WILSON BULLETIN

The official organ of the Wilson Ornithological Society, published quarterly, in March, June, September, and December. The subscription price, both in the United States and elsewhere, is $10.00 per year. Single copies, $2.50. Subscriptions, changes of address and claims for undelivered copies should be sent to the Treasurer. Most back issues of the *Bulletin* are available (at $2.50 each) and may be ordered from the Treasurer. Special prices will be quoted for quantity orders.

All articles and communications for publications, books and publications for reviews should be addressed to the Editor. Exchanges should be addressed to The Josselyn Van Tyne Memorial Library, Museum of Zoology, Ann Arbor, Michigan. Known office of publication: Department of Zoology, Mississippi State University, Mississippi State, Mississippi 39762.

Second class postage paid at Mississippi State, Mississippi and at additional mailing office.

PRINTED IN U.S.A. Allen Press, Inc., Lawrence, Kansas 66044

The gallinule *Pareudiastes* ("*Edithornis*") *silvestris* (Mayr).
From a painting by F. L. Jaques in the American Museum of Natural History.

THE WILSON BULLETIN

A QUARTERLY MAGAZINE OF ORNITHOLOGY

Published by The Wilson Ornithological Society

VOL. 87, NO. 1 MARCH 1975 PAGES 1–144

THE SOUTH PACIFIC GALLINULES OF THE GENUS *PAREUDIASTES*

STORRS L. OLSON

On 4 December 1929, a native boy on the island of San Cristobal in the Solomons carried a strange and totally unknown gallinule into the camp of a party from the Whitney South Sea Expedition consisting of Ernst Mayr, W. F. Coultas, and W. J. Eyerdam. The sight of this specimen "gave Mayr such a thrill he nearly fainted with excitement . . . had to lay off work for the rest of the day: the thrill was too much for his constitution, which otherwise is quite sound" (Coultas and Eyerdam, in Greenway 1973:150).

Some appreciation of Mayr's understandable rapture may be gained from the frontispiece which is taken from a painting done some years ago by the late F. L. Jaques and which reposed thereafter in the American Museum of Natural History. To my knowledge this is the first illustration ever published of the bird Mayr was later to name *Edithornis silvestris* (Mayr 1933).

TAXONOMY

In his original description, Mayr (1933) noticed a similarity between *Edithornis silvestris* and the now extinct *Pareudiastes pacificus* of Samoa. Later (Mayr 1949:22), he remarked that "a revision of the family Rallidae may reveal the necessity for combining [*Edithornis*] with *Pareudiastes*." Greenway (1973) also believed that this would quite probably be done. In my classification of the Rallidae (Olson 1973b), I took this step, but limitations of space prevented me from presenting many details at that time. I will take the present opportunity to offer a more complete characterization of the expanded genus *Pareudiastes*.

While *Pareudiastes silvestris* can scarcely be confused with any other rail, *P. pacificus* bears a superficial resemblance to *Gallinula*. In the following diagnosis, therefore, I have listed those characters that link the two species of *Pareudiastes* but which at the same time distinguish them from *Gallinula*.

GENUS *PAREUDIASTES* HARTLAUB AND FINSCH 1871

Included species: P. pacificus Hartlaub and Finsch (the type); *P. silvestris* (Mayr).

Diagnosis: Frontal shield flatter and thinner than in *Gallinula*, starting as a thin ridge above each nostril and produced into a small but distinct flange over the loreal area. Posterior border of shield truncate rather than rounded as in *Gallinula*. Bony nostril smaller and more rounded. Supraloreal, supraorbital, and postorbital areas with sparse, short feathers (appearing bare), differing from the uniformly feathered face of *Gallinula*. Tarsi and toes shorter and stouter than in *Gallinula*. Tail much shorter, the rectrices decomposed, the undertail coverts dark rather than white as in *Gallinula* (however, the undertail coverts are dark in the subgenus *Tribonyx* of *Gallinula*). White flank spots (characteristic of *Gallinula*, except most *G. tenebrosa* but see Cox [1973]) lacking. Breast with a decidedly bluish tinge.

I believe these characters are sufficient to separate *Pareudiastes* from *Gallinula* and to unite *pacificus* and *silvestris* in one genus. *P. silvestris* differs from *P. pacificus* in the following characters: larger size (e.g. tarsus 63.5 mm vs. 46.9 and 40.4 in two specimens of *pacificus*); bill larger and heavier; gonys with two longitudinal grooves (lacking in *pacificus*); frontal shield much larger, extending well past the eye (in *pacificus* the shield reaches only to the middle of the eye); bare area beneath the eye more extensive; bristly loreal feathers shorter, exposing more of the skin beneath; bluish tinge of breast more pronounced, extending also to the nape and mantle (in *pacificus* the dorsum is uniform dark brown). (In the rather poorly executed color plate of *P. pacificus* in Rothschild (1907), the bird is made to look much more bluish and *Porphyrio*-like than is true of the two specimens that I examined, while the plate in Hartlaub and Finsch (1871), although drawn much better, seems not bluish enough.) The differences between *P. pacificus* and *P. silvestris* are probably no more than would be expected between two well-isolated species of the same genus.

I have been able to extract the distal end of the tarsometatarsus from a damaged specimen of *P. pacificus*. This proves to be quite distinct from that of *Gallinula* (Fig. 1). In *Pareudiastes* the shaft is relatively narrower, the distal end more expanded, the inner and outer trochleae placed farther distally, the inner trochlea is not rotated as far posteriorly, the scar for the hallux is deeper, and all three trochleae are broader and less elongate. From that of *Porphyrio* (incl. *Porphyrula*), the tarsometatarsus of *Pareudiastes* differs in the slightly heavier shaft, smaller distal foramen, less developed wing of the outer trochlea, more massive inner trochlea, and less sculpted and complex scar for the hallux.

The tarsometatarsus of *Pareudiastes* can be considered as being almost perfectly intermediate between that of *Gallinula*, which is typical of most rails, and that of *Porphyrio*, which is highly specialized for walking on floating vegetation (Olson 1973a). The more bluish coloration and the smaller, more rounded bony nostril are also characters in which *Pareudiastes* resembles *Porphyrio*. The genus *Pareudiastes* might therefore be regarded as a relict group occupying a position that is morphologically and perhaps phylogenetically intermediate between *Gallinula* and *Porphyrio*.

NATURAL HISTORY

Very little is recorded about either species of *Pareudiastes* in life. Apparently all that is known of *P. pacificus* is contained in the accounts of Whitmee (1874) and Pritchard (1866). The available specimens come from the Samoan island of Savaii, but Whitmee indicates that the species also occurred

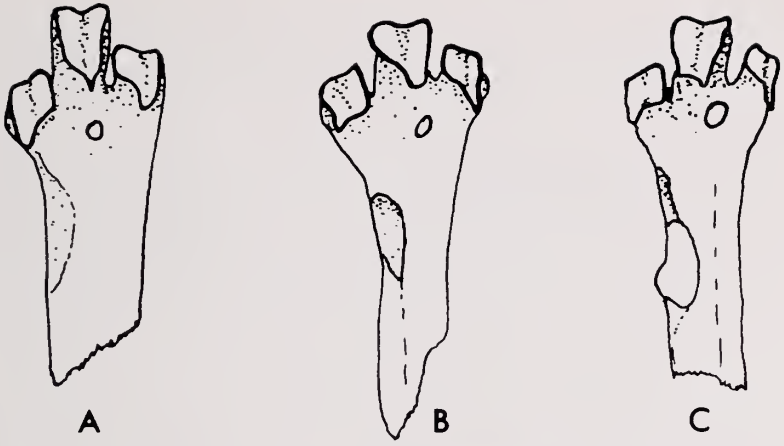

FIG. 1. Gallinule tarsometatarsi, posterior view of distal end: (a) *Gallinula chloropus*, (b) *Pareudiastes pacificus*, (c) *Porphyrio martinica*.

on Upolu. Armstrong (1932) states that *P. pacificus* was once found on Tutuila and on Tau in the Manua group, but since much in Armstrong's book appears to be unreliable, these records may be doubted.

The bird inhabited montane forest. Both Pritchard (1866) and Whitmee (1874) give *puna'e* (meaning "springer-up" according to Pritchard) as the native name of *P. pacificus*, and both state that the natives consistently maintained that the birds lived in burrows in the ground. Mayr (1945) and Greenway (1958) suggested that these statements were the result of confusion between the rail and some procellariiform. That this may not have been the case, however, is evidenced by Pritchard (1866:164). Although he never saw the bird himself, he relates that, according to the natives, the *puna'e*, when started from its burrow, "makes a long spring upwards from the ground, but having very small wings it cannot fly." This suggests that the bird was something other than a petrel. On the other hand, Whitmee (1874: 185) reports that a *puna'e* with two eggs was taken by a native from a nest on the ground "composed of a few twigs and a little grass," a description that does not correspond with the bird's reputed burrowing habits. These eggs were described as being "of much less breadth, longer, and lighter in colour" than those of the indigenous *Porphyrio*.

Hartlaub and Finsch (1871) remarked on the large eyes of *P. pacificus*, from which Greenway (1958) inferred that the species might have been crepuscular or nocturnal. Whitmee and Pritchard both indicate that the diet of *P. pacificus* consisted almost entirely of animal matter and Whitmee told of captive birds that fared poorly when fed on a vegetable diet.

While the natives esteemed the *puna'e* as food, its apparent demise is probably attributable to rats, cats, and other introduced predators. There are no authenticated records of *P. pacificus* after 1873: the Whitney Expedition failed to find it in 1926 (Greenway 1958). It has since then been presumed extinct.

Of *P. silvestris* even less is known. The type and only specimen was taken in montane forest at about 600 m in the center of San Cristobal in the Solomons. Mayr (1933) reckoned it was truly a bird of the forest and that it was quite rare. The bird is called *kia* by the natives and it is hunted with dogs: presumably it has little or no flying ability. Unfortunately, the body skeleton of the type was not saved, as this would certainly have indicated to what extent the pectoral apparatus may be reduced.

Galbraith and Galbraith (1962:22) commented that in 1953 the species was still "well-known to the natives, and apparently not rare below Nagasi," yet they failed to obtain any specimens. This rail is probably in little danger of extinction since the very steep, dense mountain forest it inhabits is virtually inaccessible and the human population of the island appears to be abandoning the mountain settlements in favor of the lowlands.

ACKNOWLEDGMENTS

I am very much indebted to Dean Amadon and the American Museum of Natural History, both for permission to reproduce the painting by F. L. Jaques that forms the frontispiece, and for access to specimens of *Pareudiastes*. For reading and commenting on the manuscript I am also grateful to John Farrand, Jr., Kenneth C. Parkes, and Dean Amadon.

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NATIONAL MUSEUM OF NATURAL HISTORY, SMITHSONIAN INSTITUTION, WASHINGTON, DC 20560. ACCEPTED 24 JULY 1974.

REQUESTS FOR INFORMATION

Canvasbacks.—Canvasbacks marked with colorful plumage dyes were recently released at key migrational concentration areas in the North Central states by wildlife research biologists of the U.S. Fish and Wildlife Service. The purpose of the color-marking program is to determine the migrational dispersal and wintering distribution of Canvasbacks staging on the Upper Mississippi River. During the 1974 fall migration, male Canvasbacks were dyed different colors at concentration areas near LaCrosse, Wisconsin, and Keokuk, Iowa. The colors used were blue, yellow, and pink. Any observation of color-marked Canvasbacks should be reported to the Northern Prairie Wildlife Research Center, P.O. Box 1747, Jamestown, ND 58401. The following information is requested: observer (name and address), date, time, location of observation (be specific), and color of the bird (be descriptive). In addition, information on the activity of the bird, size of the flock, and species of ducks associated with the marked bird would be helpful. This research on the migrational habitat and destinations of the Canvasback is part of a comprehensive investigation to identify major factors influencing the population status of this species. Any observations of these color-marked Canvasbacks would be greatly appreciated.

Birds of Gambia.—A comprehensive checklist of the birds of Gambia is currently being prepared by Mr. Jens Kirkeby and Mr. Jorn Vestergaard Jensen in cooperation with the Gambian Ornithologists' Society. It is intended that this checklist will bring together all bird records for the Gambia. Anyone having unpublished records for this area is requested to make these known to Jorn Vestergaard Jensen, Holtevej 13, DK-8000 Aarhus C., Denmark. All contributions will be fully acknowledged.

BREEDING BIOLOGY OF THE MOUNTAIN PLOVER

Walter D. Graul

The Mountain Plover (*Charadrius montanus*) is an endemic species of western North America, breeding on the shortgrass prairie mainly east of the Rocky Mountains and wintering in similar habitat from California and Texas to northern Mexico. Apart from a few anecdotal reports, detailed information on the breeding biology of the species comes from a single study (Laun 1957). In 1969, I began a study of the Mountain Plover on its Colorado breeding grounds. This paper describes various aspects of the breeding biology of the species and discusses their adaptive significance. Other aspects of the behavior of the Mountain Plover have been published elsewhere (Graul 1973a, 1973b, 1974).

STUDY AREA AND METHODS

I studied these plovers on two areas in northern Weld Co., northeastern Colorado. The major area consisted of 16 km^2 just southwest of Keota. The second area was on the International Biological Program's Pawnee Site, approximately 64 km northwest of Keota. This general area is part of the high shortgrass prairie (elevation about 1470 m) and consists of gently rolling hills with extensive flats and intermittent streams. Most observations were confined to areas covered predominantly by blue grama grass (*Bouteloua gracilis*) and or buffalo grass (*Buchloe dactyloides*), since I observed that Mountain Plovers prefer such areas. In these areas other common plants include western wheat grass (*Agropyron smithii*), fourwing saltbush (*Atriplex canescens*), and prickly pear cactus (*Opuntia polycantha*).

The climate of the area during the breeding season is hot and dry. Average yearly precipitation ranges from 30 to 38 cm, although precipitation is unevenly distributed on a yearly, seasonal, and area-to-area basis (Badaracco 1971). The mean maximum temperatures for Grover (24 km north of Keota) are: April, 16°C; May, 21°C; June, 27.2°C; July, 30°C; August, 32.2°C. The means, however, obscure the fact that the temperature commonly reaches 37.7°C in June, July and August.

I spent the following periods on the areas: 18 March–15 August 1969; 25 May–29 May 1970; 1 June–31 July 1971; 31 March–19 May 1972; 9 May–17 May 1974. Dawn to dusk observations were made throughout most of the study and were supplemented with night observations. Most observations were made from a car using a 15 to 60× spotting scope.

I captured 43 adults at the nest or with broods and marked them with combinations of colored leg bands, numbered aluminum bands, and dye. Prior to 1974 the adults were captured with either a bow trap or a drop trap. In 1974, I supplemented these trapping techniques with a mist net funnel trap and by night lighting. To avoid nest abandonment, most trapping efforts were restricted to the hatching and chick phases. Additionally, 7 adults were marked by placing "Thief Detection Powder" (Faurot, Inc., 299 Broadway, N.Y., N.Y.) in the nest cup. These birds had to be re-marked about every three days, since the dye faded rapidly.

I found 154 nests and an additional 60 broods during the study and placed colored and aluminum leg bands on 229 chicks. In 1969 the egg position in most nests was recorded using the methods described by Lind (1961) and Drent (1967).

All positive identifications of sex were obtained through collection, laparotomy, or by observing copulatory position.

ARRIVAL, EARLY SOCIAL BEHAVIOR

The birds arrive in late March and disperse onto territories. At least some adults of both sexes occupy the same territories each year. Initial pair bonds are formed and egg-laying begins in late April. In some cases, after a female completes her clutch the male assumes all parental duties and the female produces another clutch which she attends herself. Further details concerning the events leading up to the establishment of nests are presented by Graul (1973b).

NEST SITE SELECTION

Prior to nesting several potential nest scrapes are constructed on a territory as the result of courtship (Graul 1973b). Although I do not know why one scrape is chosen over others as the nest site, it is possible to examine the features at the nests. The following is an analysis of 133 nest sites observed during 1969–72.

Vegetation type.—All nests were within the general blue grama-buffalo grass community (these two species are hard to separate except when in flower), but within this community sub-communities can be defined. Seventy percent of the nests were in areas of predominantly blue grama-buffalo grass with scattered clumps of cacti and western wheat grass, and 20% were in areas of blue grama-buffalo grass and western wheat grass patches in about equal proportions. The final 10% were located in various habitat types, mostly characterized by the presence of mixed blue grama-buffalo grass and taller vegetation such as shrubs.

Since the above analysis refers to general nesting habitat, I analyzed the vegetation within 3 m of each nest to see if birds were selecting certain features within a general habitat type. Ninety-two percent of the nests were in blue grama-buffalo grass patches.

Bradbury (1918) noted that the Mountain Plover avoids tall vegetation: my observations support this contention. The mean height of the blue grama-buffalo grass is less than 8 cm in April while the other major plant species in the habitat descriptions are over 10 cm in April.

Slope of the ground.—Sixty-five percent of the nests were on ground with less than a 1° slope and another 25% were on ground with a slope of less than 2°. Only one nest was located on ground with a 5° slope, although many of the gently rolling hills have a slope of 5° or greater. Thus, although

Table 1

A Comparison of the Distance (cm) to the Nearest Cow Manure Pile Between Different Nests of the Same Bird

Sex	Nest 1 (1971)	Nest 2 (1972)	Nest 3 (1972)
M	over 91	against	–
M	33	30	–
F	61	8	–
F	over 91	against	–
F	30	over 91	10

the blue grama-buffalo grass covers many of the hills in the area, Mountain Plovers nest almost entirely on flat areas, either on top of the hills or in the valleys. The same tendency has been noted in the Three-banded Plover (*Charadrius tricollaris*) (Brown 1948) and the Double-banded Courser (*Rhinoptilus africanus*) (Maclean 1967).

Proximity to manure piles.—Fifty-five percent of the nests were within 30 cm of an old cow manure pile of at least 5 cm in diameter: 19.5% were placed against a pile: 17.5% were within 7 cm of a pile: 8% were within 15 cm: 10% were within 30 cm. To determine whether the above frequency represented actual selection I sampled the distribution of cow manure piles on my study area as follows: 120 sample points were established on a transect across the overall study area and 20 of these points were randomly selected and treated as nests. None of the sample points were within 15 cm of a 5 cm diameter manure pile and only one was within 30 cm. Thus, it appears that the birds are actually selecting nest sites near old, gray cow manure piles. Individual birds, however, are not necessarily consistent in selecting nest sites in relation to cow manure piles (Table 1), so the process of such selection is puzzling.

The tendency to nest near manure has been reported for other plovers: St. Helena Sandplover (*Charadrius sanctaehelenae*) (Pitman 1965), Black-breasted Plover (*Vanellus tricolor*) (Favaloro 1944), Kittlitz's Sandplover (*Charadrius pecuarius*) (Hall 1958), Spur-winged Plover (*Vanellus miles*) (Hall 1965), and the Lapwing (*Vanellus vanellus*) (Cott 1966). In fact, nesting near manure may be an expression of a widespread tendency among Charadriidae species to nest near conspicuous objects in general. In support of the latter statement, Bunni (1959) noted that the Killdeer nested near a variety of conspicuous objects on his Michigan study area and I have noted that they frequently nest against cow manure piles on my Colorado study area.

Presence of other birds.—Another factor probably affecting the location of nests is the presence of other birds. Interspecific aggression between

McCown's Longspurs (*Rhynchophanes mccownii*). Horned Larks (*Eremophila alpestris*) and Mountain Plovers may have some spacing effects, since these species all try to drive each other away from their respective nests.

The spatial relationship of Mountain Plover nests, at least, suggests that these nests are not placed randomly with regard to each other. Even when breeding populations were high, some areas had many nests while similar areas had few suggesting a loose colonial tendency. Within a population, however, nests were widely spaced. For instance, in 1969 I attempted to find all nests on a 64.77 ha area. At one point there were 21 nests active simultaneously on this area with the average distance between Mountain Plover nests being 140 m.

EGG-LAYING PHASE

Clutch-size and egg description.—Coues (1874) noted that sometimes a Mountain Plover nest contains four eggs, but that three normally constitute the full clutch. Completed clutches I observed included one of four eggs, 134 of three eggs, 17 of two eggs, and two of one egg.

Most eggs in my study had a dark olive ground color with many black markings, similar to the description by Bent (1929). One set of eggs was distinctive in that the ground color was reddish-brown. The black marking can be: (1) bold, large blotches; (2) fine, small specks; or (3) mixtures of the two. I have no evidence that individual females tend to lay eggs with a distinctive pattern as reported for the Dotterel (*Eudromias morinellus*) (Nethersole-Thompson 1973).

Based on 58 eggs Bent (1929) listed the average measurement as 37.7 mm × 28.3 mm. I measured 114 eggs which averaged 38.1 mm × 28.6 mm. The eggs showing the four extremes in my sample measured **42.2 mm** × 28.8 mm. **34.3 mm** × 28.0 mm, 39.6 mm × **30.2 mm**, and 39.7 mm × **27.0 mm**.

Schönwetter (1967) listed the average weight of a fresh egg as 16.5 g. I found the average weight of 25 eggs during the first week of incubation was 15.6 g with a range of 13–19 g and I found no tendency for individual females to lay eggs of similar weight.

Schönwetter (1967) tabulated several egg measurements for 34 of the 37 species of Charadriinae—the relative shape of the eggs and shell thickness are especially interesting. Schönwetter expresses the roundness of an egg (K) as length divided by width. The Mountain Plover lays a more rounded, blunt egg ($K = 1.32$) than most species of Charadriinae—only three species having a lower K value. Furthermore, there is no correlation between egg shape and clutch-size, since the mean K values for the clutch-size classes are as follows: four—1.39; three—1.36; two—1.38.

Shell thickness in Charadriinae ranges from 0.12 mm–0.22 mm with only

two species having shells as thick as 0.22 mm—the Mountain Plover and the New Zealand Dotterel (*Pluvialis obscura*). The thick shell in the Mountain Plover, at least, does not appear to be a direct function of egg size, since six species have a larger egg, but a thinner shell.

Laying behavior.—I observed four females laying eggs and the behavior was similar in each case. The female quickly approaches the nest, sits on it briefly, rises and moves off a few cm, then returns to settle in the scrape. One female repeated this sequence three times before settling on the nest. She then pumps her tail up and down several times, and may change position on the nest. Eventually, she rises 2 cm or so off the nest and slowly pumps her tail as the egg slowly appears. As the egg drops, her body rocks sideways noticeably. She then settles back on the nest and manipulates nest material with her beak briefly, and then leaves the nest quickly. Time spent on the nest in these four cases was 17, 21, 26, and 28 min. The time of laying in these cases was 06:30, 16:20, 18:30, and 19:14.

Laying intervals.—Data on the time intervals between successive eggs are scarce for the Mountain Plover. Laun (1957) reported a case of two eggs being laid in two days. I have recorded the following intervals between the laying of the second and third eggs: at least 28 hours (one record); 34–48 hours (eight records); 56–100 hours (one record); 96–108 hours (two records).

Laying periods and their relationship to weather.—Dates for the laying of first eggs in 1969 and 1971 were calculated by back-dating. With nests, the first egg date was determined at hatching time by allowing 29 days for incubation and three days for laying. With broods, the first egg date was determined by adding 32 days to the estimated age of the chicks where chick age was determined by comparing growth measurements with those of known-age chicks.

In 1969 and 1972 egg-laying began on 17 April, in 1971 on 21 April. In 1969 and 1971 the last clutch was started between 12 June and 15 June. As reported for many avian species (Immelmann 1971) rainy periods tended to inhibit laying, but laying frequently increased following such rainy periods (Fig. 1 and 2).

Inclement weather is likely during the first three weeks of April and this may be a factor influencing delay or start of laying until late April on average. A storm on 26 April 1972 produced 2.5 cm of snow which was then covered by sleet; the snow covered the ground for one day. Four clutches were initiated prior to this storm. One was abandoned; the others were unattended while covered by snow and incubation was resumed when the snow melted. I checked one egg in one of these nests two weeks later and it was fertile.

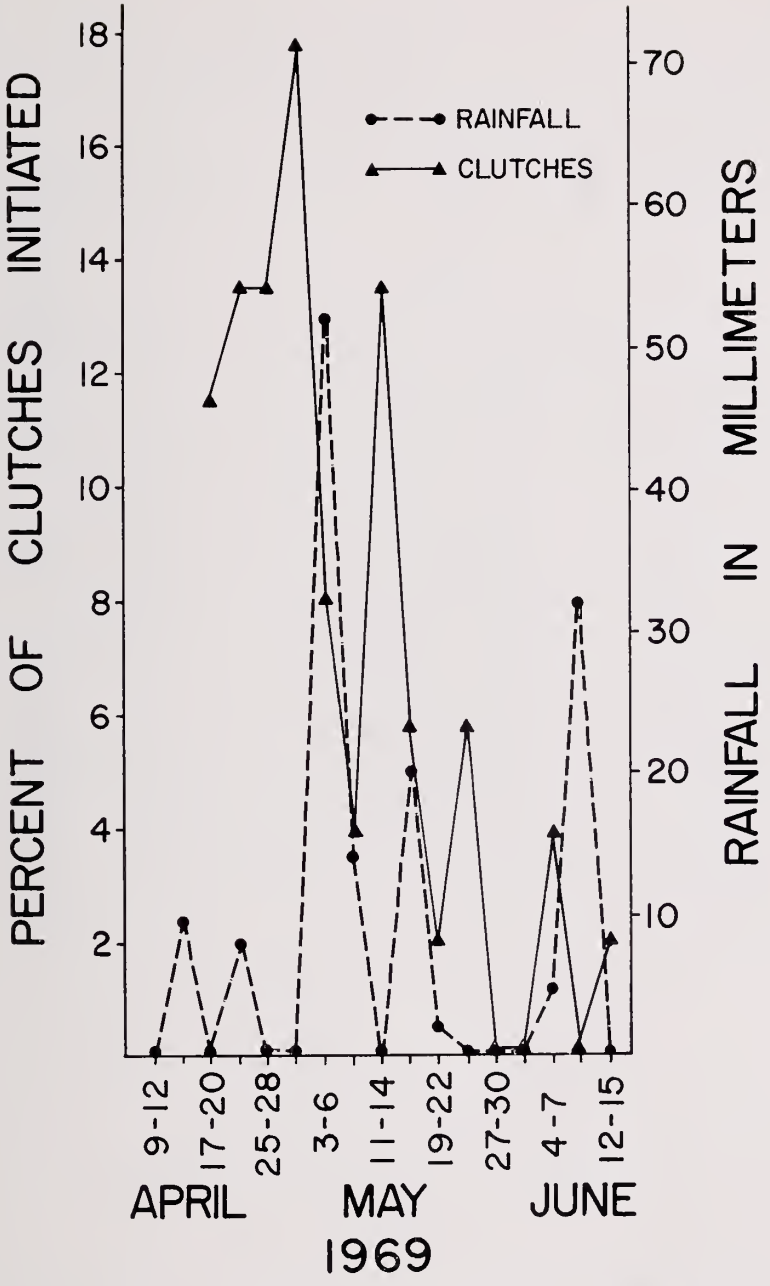

FIG. 1. Initiation of egg-laying in 55 nests in relation to rainfall in 1969.

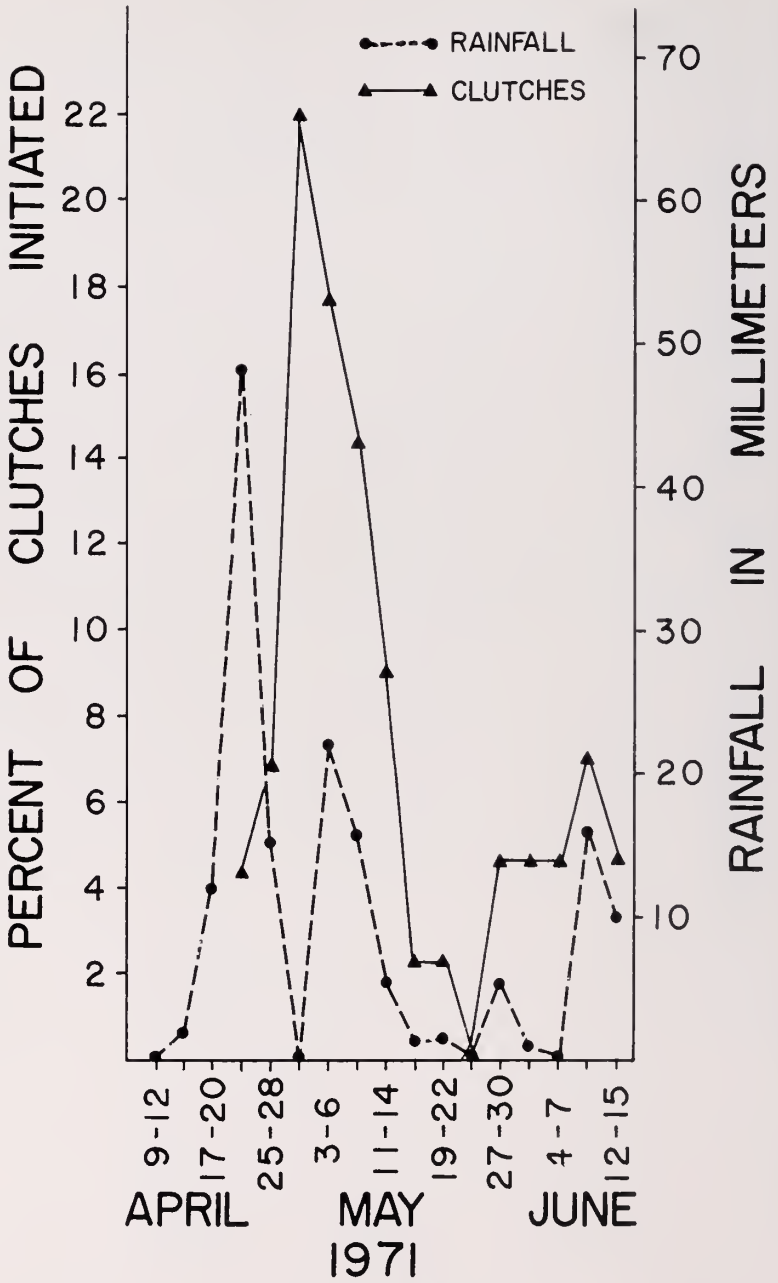

FIG. 2. Initiation of egg-laying in 45 nests in relation to rainfall in 1971.

Norton (1972) reported a set of Dunlin (*Calidris alpina*) eggs that was covered by snow for 16 hours, but hatched normally.

Weather may also be an important factor governing the end of the laying period. Most nests are initiated before mid-June, after which it commonly gets hot and dry. In 1971 June was considerably hotter and drier than in 1969 and several birds on late nests in 1971 abandoned the nests (Graul 1973b).

INCUBATION PHASE

Attentiveness.—During egg-laying the nest is attended only occasionally and attendance appears to be related to weather conditions. As in the Kentish Plover (*Charadrius alexandrinus*) (Rittinghaus 1961) and the Lapwing (Bannerman 1961), an adult will immediately come to the nest if it starts to rain, at least during the daytime. An adult will also stand over the eggs during the heat of the day. Based on six night checks it appears that adults do not attend incomplete clutches at night.

Incubation begins once the clutch is complete and the attending adult spends more and more time at the nest as incubation proceeds (Fig. 3). During the daylight hours, adults spent an overall average of 42.3% of the time on the nest in 1969, 57.8% in 1971. These figures are low when compared to other species of Charadriidae, since in most species both sexes share incubation and eggs are usually not left unattended for long periods.

The increased attentiveness in 1971, as compared to 1969, may have been related to warmer temperatures, since adults spend the highest percentage of the time on their nests during the hottest period of the day (Fig. 4). The bird does not sit on the eggs during these hot periods, but merely stands over them to provide shade. When standing over the eggs the feathers on the head and back are raised, the eggs are exposed to the air but shaded, and the bird pants. Maclean (1967) described a similar posture in the Double-banded Courser and noted that it faces away from the sun during warm periods. The Mountain Plover also tends to face away from the sun during the heat of the day (Table 2).

Night observations during the incubation phase showed an adult on the nest on 22 of 27 occasions. On three checks at separate nests when the adult (marked) was not on the nest, I found the adult within 30 m of the nest. One of these adults was not on the nest at 22:30 one night, but was on at the same time the next night and I could detect no difference in weather conditions between the two nights. Two observations suggest that the preceding cases are the result of the birds periodically leaving the nests at night rather than merely being the result of the birds walking away from the nests as I approached:

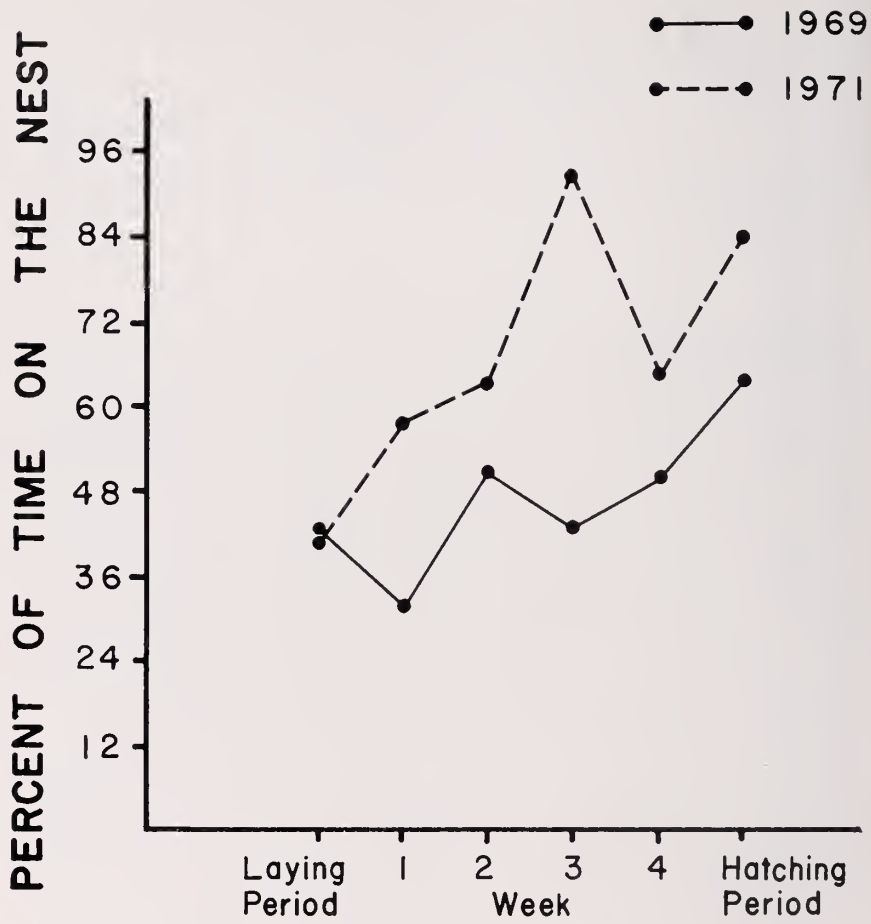

FIG. 3. Average percent of daylight hours spent on the nest by incubating adults vs. stage in incubation. Based on 727 checks of 55 nests in 1969 and 180 checks of 13 nests in 1971.

(1) when I checked birds on the nest at night with a spotlight, they either showed no signs of alarm or flew off the nest into the distance (2) in one case I purposely flushed a bird from the nest on an extremely dark night and 20 min later it was within 25 m of the nest.

Accumulation of nesting material.—When the first egg is laid there is usually no nest lining in the scrape, but the attending adult adds nest material throughout egg-laying and incubation. All sorts of objects lying near the nest may be added to the lining, certain items being more common than others. The main nesting material in 133 nests was: cow manure chips—66 nests,

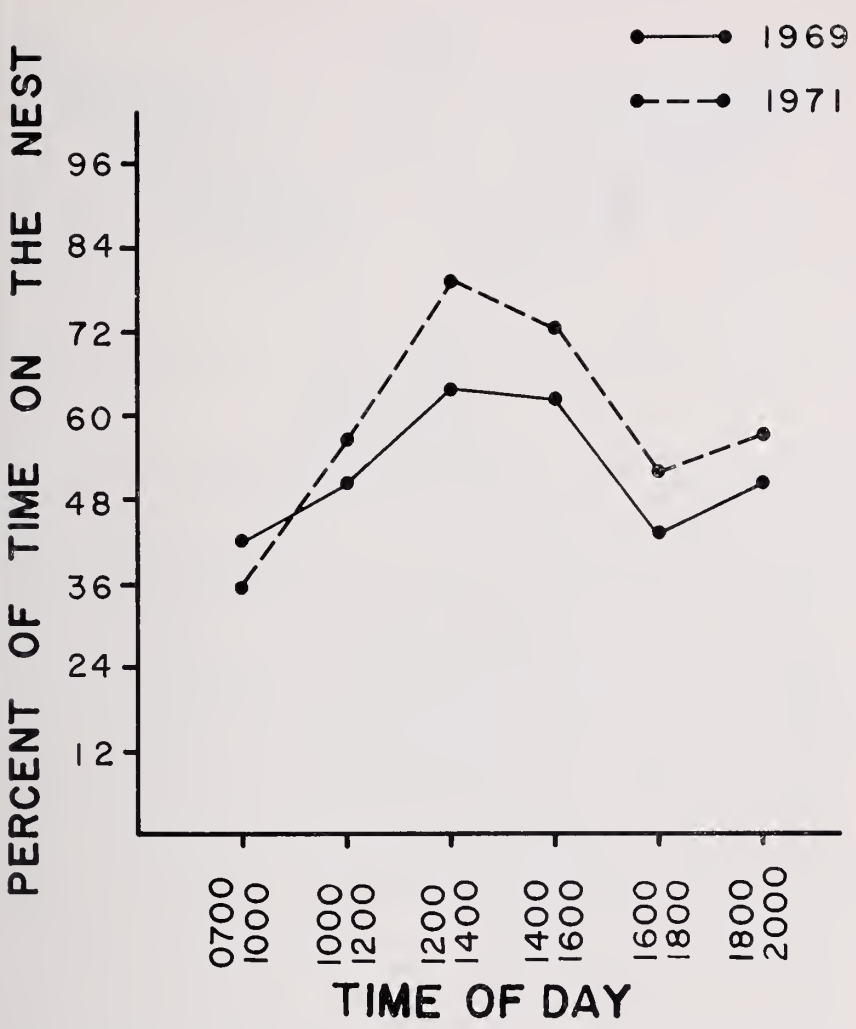

FIG. 4. Average percent of time spent on the nest by incubating adults vs. time of day (based on the visits cited in Fig. 3).

blue grama or buffalo grass rootlets—42 nests, blue grama or buffalo grass leaves—20 nests, and *Cymopterus acaulis* or *Lomatium orientale* seed pods—four nests. Less common items include rabbit manure, and two species of lichen (*Parmelia molliuscula* and *Nostoc* sp.). Although most items are lying on the ground near the nest, the birds will pull out rootlets and break chips from dried cow manure piles.

Response to human intruders at the nest.—The response of incubating

Table 2

Orientation of Incubating Adults to the Sun at Different Air Temperatures in May, 1972*

Orientation to Sun	Temperature		
	16°C or Less	Greater Than 16°C Less Than 21°C	Greater Than 21°C
Facing Sun	4	4	1
Facing Away From Sun	4	14	26
Intermediate Positions	12	6	2

* These records were obtained as the temperature rose throughout the day on three cloudless days.

birds during the day to the approach of a human is variable. Frequently the bird will quietly leave the nest while the intruder is still 50–100 m away, but on some occasions it waits until the intruder is near the nest. If the intruder does not leave, the bird may move away even more, but it will usually stay in the vicinity of the nest and perform a variety of distraction displays, accompanied by several distinct vocalizations (Graul 1974).

The frequency and duration of the distraction behavior seem to increase as incubation progresses and peak at hatching time. Occasionally, a bird with an incomplete clutch will perform distraction behavior: this has also been noted for the Killdeer (*Charadrius vociferus*) (Hiett and Flickinger 1929).

Distraction displays have been interpreted as expressions of conflict between tendencies such as fleeing, attacking, and brooding (Simmons 1953, Lind 1961). One observation of a male Mountain Plover attending newly hatched chicks dramatically illustrates the intensity of the physiological stress involved. Initially the male was brooding the chicks, but as I approached it began performing distraction displays. As it was lying on the ground with wings extended it slowly lowered its head to the ground. Soon it became motionless: I picked it up and it was limp. Some birds have been reported to feign death in such situations (Armstrong 1965), but in this case the bird was dead. I could not be sure of the exact cause of death, but the pericardial cavity was filled with blood.

The response of incubating birds to the approach of a human at night is different than during the day. At night, the birds either remained on the nest with the spotlight on them or they flew from the nest. They never performed distraction displays.

Responses to other species.—Incubating birds will attack conspecifics, other small birds and thirteen-lined ground squirrels (*Spermophilus tridecemlineatus* when they get close to the nest (usually within 3–6m). In these situations the

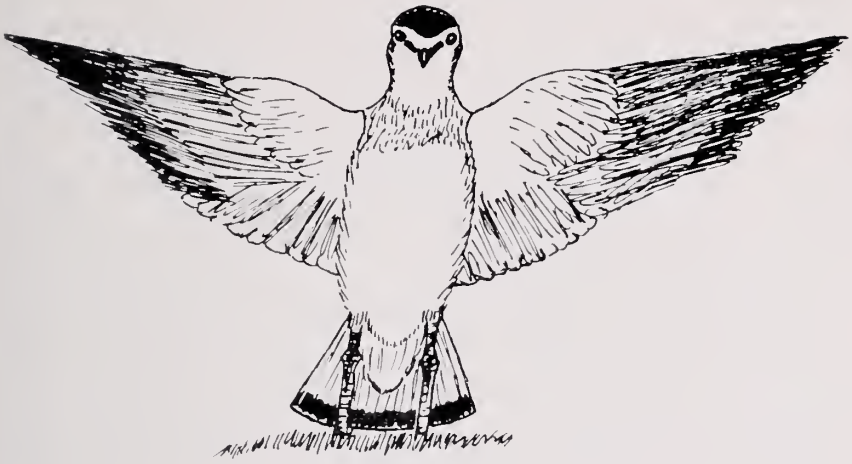

FIG. 5. Wings-out Rush Posture.

Mountain Plover, in the Wings-out Rush Posture (Fig. 5) moves quickly towards the intruder.

Cattle and other large mammals are generally tolerated until they approach within about one meter of a nest. If the large mammal gets closer the incubating bird will do one of two things: usually it will rush the intruder in the Wings-out Rush Posture, but one suddenly flushed directly towards an antelope (*Antilocapra americana*) and fluttered in front of its face. This latter behavior was also recorded by Walker (1955) in response to cattle and horses. Both reactions tended to deflect the intruders from the nest.

In 1974 I observed a kit fox (*Vulpes velox*) approach to within 5 m of an adult on a nest at dusk. The plover suddenly ran away while giving a loud series of *Ke-op* calls (Graul 1974). I scared the fox away and within 20 min the adult returned to the nest.

An incubating bird cocks its head every few minutes and looks upward. In fact, birds do this throughout the breeding season and I suspect that this behavior alerts them to the presence of potential aerial predators. When a potential aerial predator does approach a nest, the incubating bird crouches low on the nest with the head against the ground, as reported for the Double-banded Courser (Maclean 1967).

Egg losses.—In 1969, seven nests were abandoned because I removed the eggs (4) or tried to trap the adult at the nest (3); in 1971, two nests were abandoned because of my trapping attempts. These nests were not considered in determining hatching success and egg loss values. In 1969, 70% of the nests produced young; in 1971, 52.6% produced young (Table 3). The difference

Table 3

Fate of Nests in 1969 and 1971

Year	Total Nests	Hatched	Reasons for Losses			
			Human Disturbance[1]	Weather[2]	Predation	Abandoned
1969	80	52	7	10	11	0
1971	21	10	2	0	3	6*

[1] Abandoned either because I removed the eggs or tried to trap the adult at the nest.
[2] Abandoned either because of hail damage to the eggs or because the nest was covered by water.
* In one nest all eggs were infertile. The cause of abandonment in the other nests was unknown.

in hatching success between the two years can be explained by the high desertion rate in June 1971. These figures compare favorably with the 56% hatching success listed by Lack (1954) for 24 precocial, ground-nesting species.

Weather can cause a heavy loss of nests on the shortgrass prairie. One hail storm, on 5 May 1969, damaged 20 of 72 eggs in 14 of 25 active nests. One adult Mountain Plover on a nest, a Horned Lark, and a Mourning Dove (*Zenaida macroura*) were found dead, apparently killed by the hail. Such storms are not uncommon in this area, but a given storm is usually fairly localized. Cody (1971) reported one hail storm near this area that killed hundreds of birds.

Following such storms, Mountain Plovers removed damaged eggs from their nests if there was a break in the shell with a protruding edge—eggs with slightly crushed spots were not removed. If two or more eggs were damaged badly, or if the nest was flooded, the adult usually abandoned the nest. One bird removed all three eggs that were damaged by hail, and then abandoned the nest.

I assumed that when eggs were missing from the nest during fair weather they were taken by predators and, on this basis, 15.1% of 73 nests in 1969 and 15.8% of 19 nests in 1971 were destroyed by predators. I once watched a thirteen-lined ground squirrel take an egg from a nest. In the earlier mentioned case of a kit fox approaching a nest, the eggs were gone the next morning. Other potential egg predators in the area include coyote (*Canis latrans*), striped skunk (*Mephitis mephitis*), badger (*Taxidea taxus*), prairie rattlesnake (*Crotalus viridis*), and bull snake (*Pituophis melanoleucus*). Creighton and Porter (1974) found that Western Meadowlarks (*Sturnella neglecta*) occasionally rob eggs from Horned Lark and Lark Bunting (*Calamospiza melanocorys*) nests on the shortgrass prairie, so perhaps they occasionally take a Mountain Plover egg. I rarely saw Crows

(*Corvus brachyrhynchos*) and Magpies (*Pica pica*) on my study area. Bailey and Niedrach (1933) speculated that a high percentage of Mountain Plover nests were lost as a result of cattle stepping on them, but I found no evidence of such damage.

At least some Mountain Plovers will renest if they lose their eggs. In two cases marked birds renested within two weeks of losing their nests.

Probably as a result of partial predation, hail damage, and because some females lay fewer than three eggs, the average number of eggs hatched per successful nest was 2.66.

Egg rotation during incubation.—In 1969 egg movement was recorded for 30 eggs throughout incubation (Fig. 6). The eggs were rotated considerably throughout incubation, apparently as a result of shuffling by the adult bird, but during hatching they maintained a relatively stable position, usually with the pipped area upward. A similar pattern has been reported for the Ringed Plover (*Charadrius hiaticula*) (Laven 1940), and the Killdeer (Pickwell 1925). In contrast, in the Herring Gull (*Larus argentatus*) (Drent 1967) and the Black-tailed Godwit (*Limosa limosa*) (Lind 1961) eggs seem to remain in a stable position throughout most of the incubation period. The reason for these species differences remains unclear.

HATCHING PHASE

Incubation period.—Based on 13 nests the average incubation period (time from laying of last egg until it hatched) was 29 days. One clutch hatched in 28 days; three took at least 31 days. Some males do not start incubating until several days after the clutch has been completed, since they are still courting females (Graul 1973b)—this may explain the three long incubation periods.

Hatching of eggs.—The first slight crack commonly appeared on the eggs three to four days prior to hatching; a hole usually did not develop until about 12 hours before the chick emerged. After the first cracks appeared new cracks developed clockwise around the blunt end of the egg (with the pointed end towards the observer). Hatching actually occurred as the chick pushed the shell cap away from the rest of the shell. Peeping noises (Graul 1974) could be heard in the eggs up to three days before hatching.

Hatching intervals.—At 25 nests, all three eggs hatched within three hours (14 cases), eight hours (6 cases), ten hours (2 cases), 17 hours (1 case), 41 hours (1 case). Hatching, therefore, was usually synchronous, but in some cases there were considerable delays.

Egg shell removal.—Adults remove egg shells, but not always promptly as eggs hatch. In four instances where I flushed a bird from the nest during hatching it immediately removed the egg shells upon returning. The

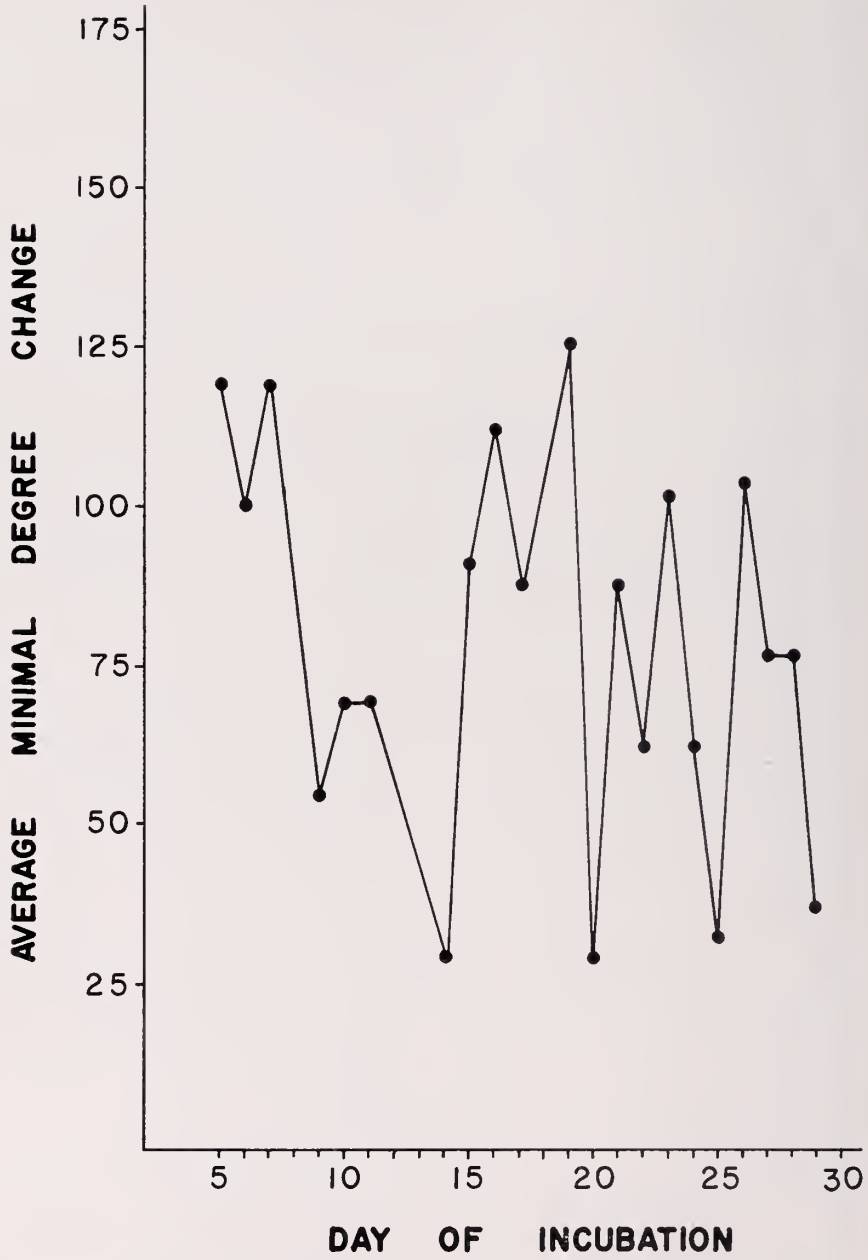

FIG. 6. The average minimal number of degrees that eggs are rotated with respect to the last nest check as a function of the stage of incubation. Based on 128 checks of 30 eggs.

Nethersole-Thompsons (1942) reported that Greenshanks (*Tringa nebularia*) and Dotterels also sometimes sit on empty shells for long periods before removing them.

Adult Mountain Plovers remove shells by grasping them in the bill and running 20–50 m before dropping them. Although the Black-fronted Dotterel (*Charadrius melanops*) (Littlejohns 1932), Kittlitz's sandplover (*Charadrius pecuarius*) (Conway and Bell 1968), and Kentish Plover (Hobbs 1972) also run away with egg shells, based on my own experience with shorebirds and numerous reports in the literature it seems that most shorebird species fly away with egg shells.

Prolonged incubation.—Occasionally one egg failed to hatch and was left in the nest when the adult moved away with the chicks. In one nest all three eggs failed to hatch and the adult, a female, maintained normal incubation for at least 43 days before finally abandoning.

CHICK PHASE

Departure from the nest.—Chicks are generally completely dry within three hours of hatching. If the last chick hatches in the morning or early afternoon and the weather is favorable, the entire brood is likely to leave the nest within three hours (8 of 10 cases). If the last chick hatches in late afternoon the brood is likely to stay in the nest until the following morning (4 cases). In rainy or cool weather (temperature under about 10°C), the brood may stay in the nest for up to 24 hours (4 cases).

During the first day after hatching the adult broods the chicks for bouts of about 4–5 min about every 12–15 min. When not brooding, the adult frequently feeds 50–100 m from the chicks. By the time the chicks are a few days old, however, the adult often stays near them while feeding. In view of the frequent absences of the adult, I never saw mixing of broods among the 229 marked chicks.

Within the first 24 hours chicks slowly pick at various objects, and by the end of this period, they sometimes successfully catch small insects. The same timing has been reported for the Killdeer (Bunni 1959).

Daily behavior patterns.—For about the first two weeks chicks are brooded much of the time in the cool early morning hours. They then spend most of their time feeding until the heat of the day, when adults and chicks of all ages seek ways to avoid the heat. This is achieved by seeking shade and/or by keeping the body off the ground.

Chicks will seek shade under small weeds or cacti, and broods, with accompanying adults, frequently congregate where there are restricted patches of shade. Such aggregations are found, for example, on weedy patches around cow watering tanks, and in the shadows of fence posts and telephone poles.

When other sources of shade are lacking, chicks stand in the shadow of the adult. I have even seen this reponse in a nearly fledged chick.

Adults frequently shade their chicks while standing on old cow manure piles. This probably has two advantages in cooling—greater exposure to wind and lower temperature of the substrate. Six wind velocity readings taken at seven cm above the ground averaged 3.5 times the average velocity from six readings at ground level. As a crude measure of substrate temperature I measured surface temperature at noon on cow piles and on adjacent ground, while the general air temperature was 25°C. Keeping the thermometer in place for five minutes in the shade, records for 10 occasions averaged 43.5°C for the ground temperature and 37.5°C for the cow pile temperature. Once I found a chick that had crawled 30 cm up into a shrub. Again, the advantage gained was presumably related to the cooling effect of the wind.

Two observations illustrate the serious consequences for these chicks of extended exposure to the sun. On both occasions, chicks under five days old were confined with the temperature at 27°C while I tried to capture the adult. All six chicks were dead within 15 min. At cooler temperatures I often confined chicks without shade for 20–30 min with no ill effects.

Aggression between the chicks of a brood appeared early and was sometimes related to competition for shade. For example, if one chick is standing in a small patch of shade and another tries to share it, one will usually peck the other until it leaves.

Response to human intruders.—Whenever I approached an adult attending a newly-hatched brood, the adult usually responded with distraction behavior and calling (Graul 1974). At least in some cases, the chicks do not crouch and freeze promptly in response to the adult alarm calls, but they do freeze if the adult leaves the immediate area. As the chicks get older they run away at the approach of an intruder instead of crouching. This transition is gradual, but appears to take place at about 10–14 days of age. Corresponding with this change in chick behavior, attending adults gradually stop performing distraction displays: they give only alarm calls with large chicks.

Brood movements.—During the first three days after hatching most broods move steadily away from their nest sites (Fig. 7). Thereafter, most broods remain within 300 m of the nest until fledging time. Two broods, however, moved over 800 m in the first two days, directly to weedy areas near cow watering tanks.

Chick losses.—Mortality is highest in chicks less than three days of age and appears constant thereafter (Fig. 8). In 1971, 16 broods of nearly fledged chicks averaged 1.37 chicks per attending adult. This average indicates that not more than 56.5% of the hatched chicks reached fledging age. This

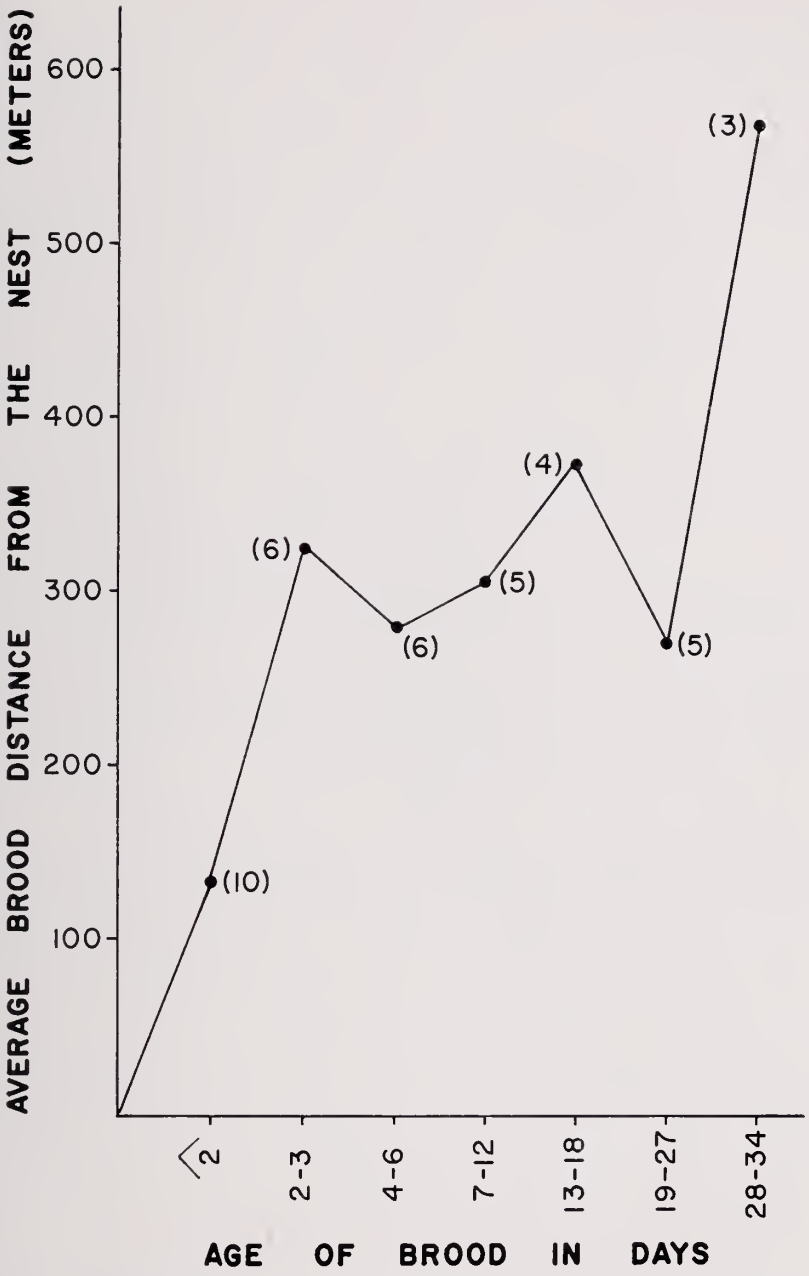

FIG. 7. The average distance broods move from their nests vs. age. Figures in parentheses represent number of broods sampled.

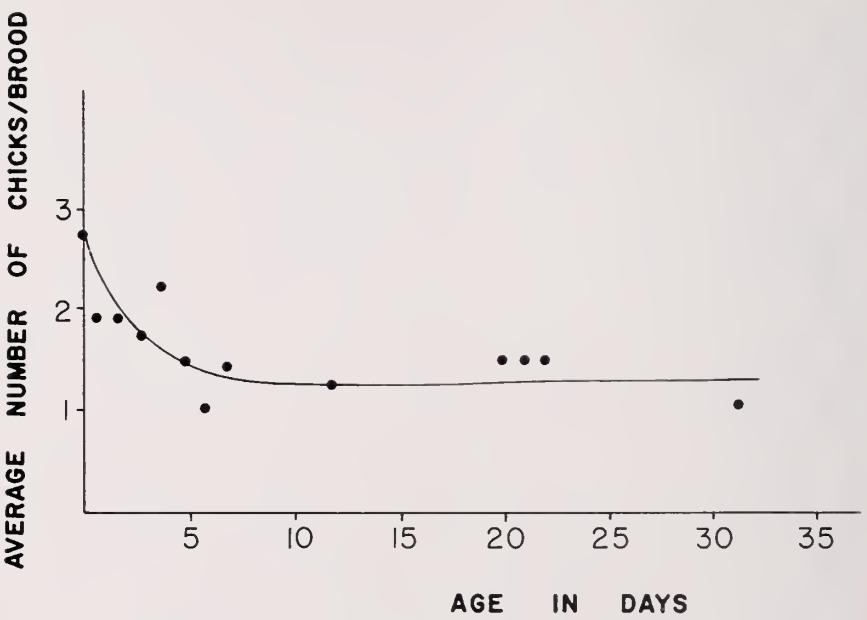

FIG. 8. The average number of chicks per brood vs. age of the chicks (N = 31), based on 1969 and 1971 data.

figure is probably high, since adults that had lost entire broods were excluded from the sample. These data agree with Laun's (1957) observations, since he rarely saw an adult with more than one large chick.

An independent estimate of fledging success was obtained by measuring the juvenile/adult ratio in flocks during the last two weeks of July. This lends support to the hatching success and fledging success for 1971. The ratio for 161 birds was one juvenile to three adults. By the end of July all chicks from nests started before 22 May should have been in these flocks and only 22.5% of the nests were started after this date. Since the success of these late nests was low, due to abandonment, I doubt that the ratio would have increased greatly: in fact, it may have decreased.

The causes of chick mortality are uncertain, but predation is no doubt partly responsible. R. Olendorff brought me the remains of one chick found in a Swainson's Hawk (*Buteo swainsoni*) nest and on one occasion I watched a Prairie Falcon (*Falco mexicanus*) take a small bird, but the prey could not be identified. One pair of Loggerhead Shrikes (*Lanius ludovicianus*) nested on my Keota study area and Sutton and Van Tyne (1937) reported that shrikes do occasionally take Mountain Plovers. An occasional Peregrine Falcon (*Falco peregrinus*) hunted on my study area, and coyotes and kit foxes are probable chick predators.

Some chicks may perish by not being able to keep up with the attending adult and other brood members. Once I saw a chick separated from its parent repeatedly attacked by another Mountain Plover adult that it had approached. Subsequently, the chick was attacked by a Horned Lark and probably would have been killed had I not rescued it.

Additional mortality may result from poor nutrition and/or disease, since I found a number of chicks that were poorly developed and underweight for their age. For instance, the average weight at six days of age was 15 g, but one six-day old chick weighed 11 g, equivalent to the average weight at hatching. In another instance, one 11-day old chick weighed 30 g, but its sibling weighed only 18 g. The small chick was still completely covered with down while its sibling had feathers on the spinal, humeral, and ventral tracts, and had some exposed primaries.

Chick fledging.—Bent (1929) described the newly hatched chick and Wetmore (1965) presented a colored photograph of one that still possessed the egg tooth. The apteria are black, a fact not mentioned in any previous description. Once the apteria are covered by feathers, however, the black coloration gradually fades and is not present in the adult.

Considerable variation exists in weights and measurements of chicks in each age class (W. Graul, in prep.), but fledging occurs at about 33–34 days of age, where fledging is defined as being able to fly at least 100 m. The fledging period is similar to that recorded for other plover species: Lapwing, 33 days; Dotterel, 31 days (Witherby et al. 1941); European Golden Plover (*Pluvialis apricaria*), 33 days (Bannerman 1961).

FALL FLOCK PHASE

In 1969, the first small flocks were observed in early July, but flocking began in mid-June. 1971. I watched the formation of these flocks in detail in 1971. As the heat of the afternoon increased, single birds would move about until they encountered others. This resulted in groups of up to four plovers resting in the shade near each other. As evening approached, however, aggression increased and birds would disperse to feed.

In both 1969 and 1971 the flocks gradually increased in size to an average of about 35 birds in late July. Two juveniles were seen in such flocks at distances of 1500 m and 3000 m from their hatching sites. In one case a flock was flushed and one marked juvenile (44 days old) stayed behind with an adult. The latter was presumably the parent, since it gave a series of alarm calls before both birds flew after the flock. Apparently not all families flock together, however, since on five occasions I have seen a fledged juvenile alone.

Flocks spend the heat of the day resting in shade, especially under weeds near cow tanks. When these flocks disperse to feed, low intensity aggressive

encounters develop and at times the aggression seems to spread throughout the flock (Graul 1974).

Flocks continue to increase in size until mid-August. By this time they begin to leave the area and flocks can be seen flying in the wheeling, dipping, precision maneuvers typical of shorebirds. Flocks are still in the Weld Co. area in September, but these may represent birds from other breeding areas. Nancy Hurley estimated 2500 in a flock on 23 September 1972, but apparently this is an exceptionally late record (R. Ryder, pers. comm.).

Birds of the year can be distinguished easily from adults in these flocks. The body coloration of the young birds resembles the spring plumage of adults except that black crown and lore lines are absent, and instead their crowns have a finely striped appearance. Adults in these flocks are in the process of losing their black facial markings (this actually begins during nesting), and bright rusty colored feathers are appearing on the back.

DISCUSSION

In deserts and semi-arid areas species must cope with certain predominant features: aridity, heat, high solar radiation, irregular precipitation patterns, and sometimes strong wind conditions (Serventy 1971). Additionally, ground-nesting birds in all habitats must evolve special anti-predator adaptations, since they are particularly vulnerable to predation (Lack 1968). In the preceding sections various aspects of the Mountain Plover's breeding biology have been described and compared to other species. These comparisons will be used to argue that the semi-arid features of the shortgrass prairie have had a major impact on the evolution of the Mountain Plover.

Adaptations to climate.—The shortgrass prairie has a harsh climate, and apparently because of the high probability of severe weather in April and extremely hot, arid conditions in summer, the Mountain Plover laying period has been condensed to about a 60-day period. To maximize reproduction within this period these birds have evolved numerous mechanisms that reduce the effects of the aridity, heat and intense solar radiation. Of special importance are restriction of most activity to early morning and late evening periods, seeking shade during the heat of the day, and standing on cow manure piles. As in many desert birds, independence from free water is a fundamentally important adaptation (Fisher et al. 1972).

Shading by the adult during the heat of the day must be of vital importance in reducing effects of high temperatures and high solar radiation on both eggs and chicks. Olendorff (1972), for instance, reported that on the shortgrass prairie three young were produced at shaded Ferruginous Hawk (*Buteo regalis*) nests while only 1.71 were produced at unshaded nests, the difference attributable to addled eggs in the unshaded nests. Standing over eggs or

chicks must produce heat problems for the adults, however, and these are eased by raising the dorsal feathers, panting, exposing the legs, and facing away from the sun. The latter behavior was noted by Maclean (1967) in the Double-banded Courser and has been discussed in detail for other species by Drent (1972).

Two physical characteristics of Mountain Plover eggs seem likely to be adaptations that reduce water loss at high temperatures and/or aid in heat retention at low temperatures: rounded egg (low surface to volume ratio), and thick egg shell. These adaptations may be especially important, since incubating adults spend so much time off nests. Being off the nests so much may, in turn, be necessary to allow the adults to feed for prolonged periods. This might be particularly important in the Mountain Plover, since I have argued elsewhere (Graul 1973b) that food supplies (insects) are sometimes extremely low on the shortgrass prairie.

The black skin of the chicks probably has evolved in response to the high solar radiation and/or the cool temperatures in early morning. Three possible explanations for the black coloration exists. Many desert animals possess black coloration (Schmidt-Nielson 1964) and black can be an efficient protective coloration in desert areas, since it allows an individual to blend into existing shadows (Serventy 1971). This interpretation, however, does not explain why the black is restricted to the apteria and why such altricial species as Mourning Dove and Yellow-billed Cuckoo (*Coccyzus americanus*) have black skin, since altricial chicks do not generally rely on protective coloration. It seems more likely that the black coloration might allow small chicks to absorb solar radiation during cool periods of the day (Heppner 1970; Lustick 1969, 1971; Ohmark and Lasiewski 1971). This again might be particularly important if food is sometimes a limiting factor on the shortgrass prairie. Alternatively, black skin might act as a shield against ultra-violet radiation (Porter 1967).

One mechanism has apparently evolved in response to the severe storms that sometimes produce heavy rains and hail: covering the eggs when it starts to rain. Nesting on flat areas may be an adaptation to heavy rains, since this would reduce the chances of a nest being subjected to heavy runoff, as suggested for the Three-banded Plover (Brown 1948).

Anti-predator adaptations.—Several features presumably have evolved to reduce the chances of predation in general: coloration of eggs and chicks (Cott 1966), coloration of the adult (Graul 1973a), egg shell removal (Tinbergen 1967, Nethersole-Thompson 1973) and removing damaged eggs, nest sites in open areas (Maclean 1967, Klomp 1954), and dispersed nesting (Tinbergen 1972). The tendency for nests to be placed near cow manure piles may serve a disruptive coloration function, or it may aid birds in re-

locating their nests. It is doubtful that other advantages would be incurred by nesting near cow piles; old piles probably do not produce an odor to mask the scent of the nest and they are not used as feeding sites.

The tendencies to attack any nest intruder that does not pose a threat to the attending adult (small birds, thirteen-lined ground squirrel, cattle, antelope), and to perform distraction displays or flee when the intruder could harm the adult (man, kit fox) seem particularly adaptive. The increase in distraction behavior as incubation progresses is to be expected, since the chances of the parent raising a new brood decrease as the season progresses (Drent 1967). After hatching selection has apparently favored distraction behavior decreasing as the ability of the chicks to protect themselves increases—simultaneously, small chicks freeze at the approach of a potential predator, but older ones run away.

SUMMARY

A marked population of Mountain Plovers was studied in northern Weld Co., Colorado during parts of the five breeding seasons of 1969–72 and 1974. Special attention was given to breeding adaptations in relation to the arid, shortgrass prairie habitat.

Nests were found on flat, open expanses of blue grama or buffalo grass, frequently near old cow manure piles. Nests were initiated in late April with egg-laying terminating in mid-June. Eggs are normally laid at 1–2 day intervals with some extreme delays (4 days) recorded. The normal clutch was three and eggs averaged 38.1 mm × 28.6 mm with an average weight of 15.6 g. The eggs have a relatively rounded shape and thick shell. The daily attentive period was relatively short and the incubation period averaged 29 days. Eggs are rotated during incubation, but not during hatching. Slight cracks appeared 3–4 days before hatching and noises were emitted by the hatching chicks.

Seventy percent of the nests in 1969 and 52.6% in 1971 produced young. Predation accounted for 15.1% of the egg losses in 1969 and 15.8% in 1971. Weather accounted for 13.7% of the losses in 1969, mainly a result of hail damage. Badly damaged eggs were removed as were egg shells at hatching time.

Adults perform distraction behavior during incubation and with chicks. One adult died as an apparent response to stress during a distraction display performance. Although adults performed distraction behavior in the presence of man, they frequently attacked other intruders.

Most chicks were raised within 300 m of the nest and mortality was highest within three days of hatching. Chicks fledged at 33–34 days, but not more

than 56.5% of the chicks reached the fledging stage in 1971. Flocking began in mid-summer and flocks began leaving in August.

Many characteristics of this species appear to have evolved in response to (1) high summer temperatures, intense solar radiation, and aridity, (2) sudden storms, (3) predators, (4) fluctuating food levels.

ACKNOWLEDGMENTS

My 1969–72 field work was supported by a National Institute of Health Training Grant (No. 2 T01 GM01779), a Chapman Fund Grant, and a Sigma Xi Grant-in-Aid, while I was a graduate student at the University of Minnesota. My 1974 work was funded by a Faculty Research Grant administered by the University of North Carolina–Charlotte. I am indebted to David Parmelee, who provided the initial encouragement for this research; Frank McKinney, who offered guidance throughout; and Scott Derrickson, who commented on the manuscript. Ronald Ryder kindly made numerous facilities available to me at Colorado State University and many personnel at the International Biological Program's Pawnee Site helped me in various ways.

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nongame section, colorado division of wildlife, 6060 broadway, denver 80216. accepted 5 sept. 1974.

NEW LIFE MEMBER

Patricia Faye Greenig is now a life member in the Wilson Ornithological Society. Mrs. Greenig is employed as a school psychologist in Verona, New York. As a lay naturalist, she is interested in supporting conservation and ornithological research. She belongs to the National Audubon Society, the Onondaga Nature Center, and numerous professional associations in Psychology. She received her Bachelor's Degree at Hunter College of the City University of New York and a Master's Degree from Vassar College. Mrs. Greenig is married to Robert M. Greenig; they have one son.

ECOLOGICAL ASPECTS OF AVIAN BILL-SIZE VARIATION

Mary F. Willson, James R. Karr, and Roland R. Roth

Ecologists and evolutionists have made various attempts to associate variation in the size of anatomical structures with ecological characteristics of organisms. The attempts have met with varying degrees of success. (e.g., Van Valen 1965, Willson 1969, Soulé and Stewart 1970, Grant 1971, Pulliam 1973, Rothstein 1973). Problems associated with studies of morphological variation have been discussed from several points of view in the above papers and by Van Valen and Grant (1970), Soulé (1971, 1972), Horton (1972) and others. We have attempted an analysis of variation in bill size of bird species known to occur together in the breeding season in east-central Illinois and for which some of the autecology is known. Basically we sought to relate the degree of variation with (1) feeding ecology—specifically foraging strategy, food habits, foraging behavior, and foraging stratum; (2) type of habitat—i.e. grassland, shrub, forest; (3) seasonal movement patterns; (4) body size; (5) the number of sympatric species in a guild of ecologically similar species (Root 1967); and (6) width of habitat niche. In addition, we analyzed the variability in one bill dimension with respect to that in other bill dimensions.

METHODS

The list of 66 species to be analyzed was obtained from breeding bird censuses (excluding owls) of 24 study areas in Champaign, Vermilion, and Piatt Counties in Illinois (Roth 1967, Karr 1968, Willson 1974). One more species, *Ammodramus henslowi*, was added for analysis of a successional series summarized in Roth (1967). The bills of these species were measured, by MFW, in three dimensions: length from the posterior edge of the nostril to the bill tip and depth and width at the anterior margin of the nostril.

More than 30 specimens were measured for all but four species which were represented by more than 20. In all cases, at least 10 of each sex were measured. The total sample exceeded 2800. Measurement error was not analyzed, but errors were consistently small. We used specimens collected in Illinois when available, but in many cases we had to use specimens from other midwestern states and adjacent parts of Canada. A table of means and standard errors is available from MFW and will be on file with the article in the Josselyn Van Tyne Memorial Library at the University of Michigan. Except for Bobwhite (*Colinus virginianus*), samples were comprised primarily of spring and summer specimens. The problems of using specimens taken over such a broad area and long time span, as represented by museum collections, are obvious but unavoidable: the practical difficulties of capturing and measuring sufficient numbers of birds on our study areas were plainly prohibitive. Few of the specimens used in this study were labeled accurately as to subspecies, according to one of the museum curators, so this taxonomic distinction was ignored.

TABLE 1
NUMBER OF SPECIES ASSIGNED TO EACH GUILD OR OTHER CATEGORY

Category	N	Category	N
Feeding ecology		Habitat[a]	
Foraging strategy		Grassland	7
Searcher	52	Shrub	28
Pursuer	14	Forest	30
Food habits		Seasonal movement patterns	
Omnivore	23	Summer resident	48
Insectivore	43	Permanent resident	18
Foraging Stratum		Body size	
Bark	5	0–3 g	1
Ground	15	3–6 g	1
Low	22	6–12 g	12
Medium	8	12–24 g	21
High	6	24–48 g	12
		48–96 g	12
Foraging behavior		96–192 g	5
Bark drill	4	> 192 g	2
Bark glean	4	Guild size	
Ground glean	15	1 species/guild	36
Foliage glean	34	2 species/guild	18
Sally	9	3–4 species/guild	12

[a] *Sturnus vulgaris* which nests and feeds in different habitats omitted from this set.

Assignment of the bird species to guilds or other ecological categories (Table 1, Appendix 1) was based on several information sources. In cases in which species could fall into more than one category, we chose the primary one for classification. Category designations and criteria follow Karr (1971) for the most part. References for body weights can be found in Willson (1974). Guild assignments and seasonal movement patterns are based on our own local field experience with most of the species. When questions arose, we supplemented those data with material from Bent (1919–1968), Martin et al. (1951), and other relevant literature. Readers might feel inclined to alter some of these assignments (e.g. Mockingbirds also sally), but because we have tried several different arrangements ourselves, we believe that such alterations will not change the major results of this analysis.

Two measures of the variability in bill dimensions were used in our study: (1) sexual dimorphism in bill size, indexed both by the frequency of occurrence and by the degree of bill size differences (the degree of difference was measured by a ratio of larger : smaller bill size); and (2) continuous variation, indexed by the variance of the logarithms of the measurements (Lewontin 1966), computed for the species sample as a whole and for each sex separately (this index is scaled so that relative variability may be compared for structures of different absolute sizes).

Statistical procedures included the use of t-tests for differences between means of males and females, Mann-Whitney U-tests for differences in continuous variation and degree of

dimorphism between ecological categories and G-tests with Yates correction (Sokal and Rohlf 1969) for differences in frequency of dimorphism. In all cases the 5% level of significance was used.

SEXUAL DIMORPHISM IN BILL DIMENSIONS AS RELATED TO ECOLOGICAL FACTORS

Feeding ecology

Occurrence of dimorphism.—We found no significant differences among categories of foraging strategy or food habits. For foraging stratum, bark users were more often dimorphic (80%) in bill length than low- or high-foliage users (18% in each), and in bill depth than high-foliage users (12%). For foraging behavior, bark-drillers were more often dimorphic (100%) in bill length and depth than ground gleaners (31% in both dimensions), foliage gleaners (25% in both dimensions) and salliers (length—0%, depth—22%). Twenty-four other comparisons were not significant.

Degree of dimorphism.—Data can be averaged in two ways, over all species and over just the dimorphic species. Considering all species, no significant differences were found among foraging strategies, food habits, or foraging stratum. For foraging behavior, bark-drillers were more dimorphic than foliage gleaners (length and depth) and salliers (length, and probably depth: $p < .055$). Twenty-seven pair-wise comparisons were not significant. When only dimorphic species were considered, none of the 30 comparisons was significant.

Habitat

Frequency of dimorphism.—Grassland species (86%) are more often dimorphic in at least one bill dimension than are shrub (50%) or forest (38%) species, but the difference is not statistically significant, largely as a result of the small number of typically grassland species. Shrub species are significantly more often dimorphic than forest species. If icterids are omitted, grassland species are significantly more often dimorphic than forest species.

Considering each dimension separately: for length, grassland species (71%) are more frequently dimorphic than either shrub (18%) or forest (26%) species; for depth (79%, 29%, 29%) the differences are not significant statistically; for width, shrub species (32%) are dimorphic more often than forest species (19%), but grassland species, while very frequently dimorphic (43%), are not significantly more so than forest or shrub species. Any trends that might be suggested here disappear if icterids are omitted from the analysis.

Degree of dimorphism.—Considering all species in each habitat type, or considering only the dimorphic species, the degree of dimorphism is similar in all habitat types.

Seasonal movement patterns

It can be argued that permanent residents are more likely to be variable than are migrant species. Conceivably, the migrants (summer residents) can select habitats or micro-habitats in their winter and summer ranges that are more similar for foraging than can year-round residents in a single area. Or, conversely, migration may involve changes in food habits or foraging behavior (see Karr 1971, for examples) and increased morphological variation.

Frequency of dimorphism.—Frequency of dimorphism in length and width are not significantly different, but permanent residents are more frequently dimorphic in bill depth than are summer residents.

Degree of dimorphism.—Considering all species, permanent residents are more dimorphic than summer residents for bill length and depth. For dimorphic species only, no bill character showed significant differences.

Body weight

Frequency of dimorphism.—No significant differences were found among the size classes for bill length. Large species (> 192 g) were more frequently dimorphic for bill depth than 12–24 g birds. For bill width large species (> 192 g) were more frequently dimorphic than 6–12, 12–24, and 48–96 g species.

Degree of dimorphism.—Of those size classes with more than one species the 96–192 g and > 192 g species were significantly more dimorphic for bill length than 6–12, 12–24, 24–48 g species. Nine other pair-wise comparisons were not significant. For bill depth, birds larger than 192 g were more dimorphic than 6–12, 12–24, and 48–96 g species. Twelve other pair-wise comparisons were not significant. For bill width, 48–96, 96–192, and > 192 g species were more dimorphic than 12–24 g species and > 192 g species were more dimorphic than 6–12 g species. Eleven other pair-wise comparisons were not significant.

For dimorphic species only, there were no significant differences in degree of dimorphism. The small number of species in each category often made significance at the .05 level impossible.

Size of guild

As the number of potential competitors, as defined by similar ecologies, increases among ecologically sympatric species, reduced morphological variation might be expected (Willson 1969, Rothstein 1973). To test this suggestion we constructed a three-dimensional contingency table in which food habits, foraging behavior and foraging stratum were the three dimensions used to compare guilds. We then compared sets of guilds with one, two, or more than

two members. No significant differences in dimorphism were found between "crowded" and "uncrowded" guilds.

Width of habitat niche

McNaughton and Wolf (1970) and Rothstein (1973) have explored in detail the suggestion that more abundant species have broader niches, or that species with broader niches are likely to be more abundant.

Our measure of width of habitat niche should be taken as a first approximation until more precise measures are available. We determined the percent vegetation cover (PCVC) in each of the three strata for all study areas as in Karr (1968) and Willson (1974), and summed over all strata. The study areas were then ranked from low to high PCVC, and the distribution and abundance of each bird species plotted on this gradient. Habitat-niche width was then indexed in two ways: by the range of PCVC occupied (five categories), and by the area under the abundance curve (large, medium and small "niche size").

Frequency of dimorphism.—Not one of 30 possible comparisons was significant.

Degree of dimorphism.—For dimorphic species alone, no significant differences appeared. For all species, only one comparison was significant.

Thus, there seems to be no relationship between width of habitat niche and bill-size variation.

CONTINUOUS VARIATION IN BILL DIMENSIONS AS RELATED TO ECOLOGICAL FACTORS

No consistent patterns in the amount of variability appeared in the comparisons of foraging strategy, food habits, foraging stratum, foraging behavior, habitat set, seasonal movement pattern, guild "crowding," or width of habitat niche. Occasional differences of statistical significance appeared, but the biological significance of these is obscure.

For body weight, over 29% of the tests were significant, more than expected at random. In general, larger size classes (48–192 g) are relatively more variable than smaller classes (6–48 g), but there are a number of exceptions, and furthermore there is no evidence of any correlation of size increment with variance.

Our series of habitats mimics a successional series in structure, and showed no trends of increasing or decreasing continuous variation. We also used an actual successional series, composed of over 20 years of breeding bird censuses on a "forest-edge" study area (Roth 1967). During this time the area changed from open pastureland with scattered trees and shrubs to a dense late shrub-forest habitat. Mean continuous variation by species and weighted by species

abundances showed no successional trend. Such an analysis could be a test of the hypothesis that niches become narrower as succession proceeds (Odum 1969). If so, the hypothesis is not supported by our results. However, the test requires the assumption that variation of bill size reflects niche width. That assumption may be inaccurate.

RELATIONSHIPS AMONG BILL DIMENSIONS

No one bill dimension tended to be more variable or to vary more often than any other.

The variance of each bill dimension was regressed on all others, but no significant product-moment correlations were evident in any of the 6 comparisons, even when the few species with unusually high variances were excluded. This indicates that selection on variability, if any, operates independently on the three bill dimensions.

DISCUSSION

Nearly 1000 tests of statistical significance were made during the course of this study in an effort to determine the ecological circumstances likely to be associated with variability in bill size. Of those, about 9.5% were significant at the 5% level, more than would be expected by chance alone ($\chi^2 = 13.43$, $p < .001$). The only ecological classification that gave more significant tests than would be expected by chance alone was continuous variation by size ($\chi^2 = 28.6$, $p < 0.001$). The irregular pattern of significant results suggests a spurious cause. Conceivably, measuring error might be relatively large on small species rendering tests of variation among the size classes ineffective (Sokal and Rohlf 1969:15). Similarly, t-tests and measurement of dimorphism may be affected by this problem. If statistical significance is ignored and only the direction of the differences is considered, no significant trends emerge.

The results presented here differ notably from those of Rothstein (1973). He found a positive correlation of morphological variability and abundance in a carefully selected example, and argued that wide niches may be expected to support larger populations than narrow niches. However, this argument is not necessarily true. One can imagine a species with a very broad niche (on some particular dimension) which is held at low population densities because resources have been reduced by interspecific overlap and competition. The concept of diffuse competition (MacArthur 1972:29) describes such a situation. We found no relationship between bill-size variation and abundance or width of habitat niche. It is possible that sampling problems or our choice of niche dimension (i.e. habitat) obscured the true relationship, but it seems more likely that the basic assumption of a relationship between abundance

and niche width needs to be refined. In particular, population density, intraspecific competition, and resulting dispersion patterns seem likely to be important.

Tests of niche width with respect to geographical (rather than ecological) sympatry have no necessary validity (Soulé 1972), although habitat restriction in areas of geographic overlap *may* be associated with restricted morphological variance. A more powerful test of the possible effects of present competitors would employ coexisting species. Insofar as this was possible with our samples, no such effect could be shown.

Only a few associations of ecological characters with bill size variability were found. (1) Species that feed from bark, especially bark drillers, are more frequently dimorphic than other species in bill length and depth. Sexual differences in morphology (e.g. Selander 1965) and in behavior (e.g. Willson 1970, 1971; Reller 1972) are well-known for woodpeckers. (2) Permanent residents are more frequently dimorphic in bill depth than summer residents, and more dimorphic in length and depth when all species are considered. When only dimorphic species are tested, the degree of dimorphism is not significantly different. The 10 species of permanent residents which are dimorphic include three bark-drillers, and four other species that are bark-users at least in winter. Only one bark-user among the permanent residents is not dimorphic. (3) Frequency and degree of dimorphism may be higher in large-bodied species than in small ones. All of these associations may be a function of a restricted resource base, either as a limited substrate in the case of bark feeders (see also Orians and Willson 1964), perhaps especially in winter, or as a limited food supply for large birds (e.g. Schoener 1965, 1968).

Our failure to find other notable correlations of autecology with morphological variation is discouraging but perhaps instructive (see also Soulé 1972).

Certain difficulties of measurement and of sampling may contribute to the problems of the study. The use of an arbitrary reference point, such as the nostril, for measurements might well obscure real differences because the location of the nostril itself is probably responsive to selection pressures. However, most studies of morphological variation with reference to niche size would encounter this problem, although the difficulties are reduced by studying restricted taxonomic units. In addition, construction of our samples from museum collections meant that in almost all cases it was essential to pool specimens from different times and places; thus, if ecotypic (Pulliam 1973) or temporal differences (Fretwell 1972) occur for any species, our values are inaccurate. The severity of this problem is untested.

There are, of course, a variety of sometimes conflicting selective pressures affecting the evolution of bill size. A very clear case is provided by the Icteridae in which some species probably are sexually dimorphic due, in part,

to sexual selection (Selander 1965). Furthermore, a consideration of morphology, even with behavioral categorizations, can easily neglect real and important behavioral differences in exploiting resources.

It is likely that bird species may carry with them phylogenetic constraints (Karr and James, in press) such that members of certain taxa may be locked into certain patterns of variation: studies of more restricted taxa would alleviate this problem. We did note, however, that separate consideration of passerines and nonpasserines did not significantly improve our results and that intraspecific variability was not a function of the number of ecologically sympatric congeners.

Problems of sampling and of compound selective pressures may preclude much success of a generalized venture such as ours. We have not attempted to test the "morphological variation model" so much as to use it: if the model is validated, it seems likely that its utility will be found primarily in situations where the biological variables, especially population structure, can be better defined.

SUMMARY

Consistent, significant associations of morphological variation in avian bill dimensions, measured by continuous variation and by sexual dimorphism, and autecological characteristics were few. Species with a limited resource base may be more frequently sexually dimorphic in bill size, and the frequency of dimorphism may change with habitat structure. Problems of this approach are discussed.

ACKNOWLEDGMENTS

For the loans of specimens we are grateful to the Chicago Museum of Natural History, the University of Kansas Natural History Museum, the University of Michigan Museum of Zoology, the American Museum of Natural History, the U.S. National Museum, and the Illinois Natural History Survey. The University of Illinois and Purdue University provided financial support for analyses of data. T. W. Schoener and R. H. MacArthur supplied critical comments and encouragement; the comments of the reviewers were helpful.

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PROVISIONAL DEPT. OF ECOLOGY, ETHOLOGY, AND EVOLUTION, VIVARIUM BLDG., UNIV. OF ILLINOIS, CHAMPAIGN, IL 61820; DEPT. OF BIOLOGICAL SCIENCES, PURDUE UNIVERSITY, WEST LAFAYETTE, IN 47907; DEPT. OF ENTOMOLOGY AND APPLIED ECOLOGY, UNIV. OF DELAWARE, NEWARK, DE 19711. ACCEPTED 3 JUNE 1974.

Appendix 1. Species Used in the Comparisons, Occurrence of Sexual Dimorphism (+) and Categorical Assignments.

Species	Sexual Dimorphism[a]			Habitat[b]	Food Habits[c]	Foraging			Body Wt. Class (g)
	L	D	W			Strategy[d]	Stratum[e]	Behavior[f]	
Bobwhite (*Colinus virginianus*)	–	–	–	S	O	S	G	G	96–192
Ring-necked Pheasant (*Phasianus colchicus*)	+	+	+	G	O	S	G	G	> 192
American Woodcock (*Philohela minor*)	+	+	–	S	O	S	G	G	> 192
Mourning Dove (*Zenaida macroura*)	–	–	–	S	O	S	G	G	96–192
Yellow-billed Cuckoo (*Coccyzus americanus*)	–	–	–	S	I	S	M	G	48–96
Whip-poor-will (*Caprimulgus vociferus*)	–	–	–	S	I	P	H	S	48–96
Ruby-throated Hummingbird (*Archilochus colubris*)	+	–	–	F	O	S	M	G	< 3
Red-bellied Woodpecker (*Centurus carolinus*)	+	+	+	F	I	P	B	D	48–96
Red-headed Woodpecker (*Melanerpes erythrocephalus*)	+	+	+	F	I	P	B	D	48–96
Common Flicker (*Colaptes auratus*)	–	+	–	F	I	P	G	G	96–192
Hairy Woodpecker (*Dendrocopos villosus*)	+	+	+	F	I	P	B	D	48–96
Downy Woodpecker (*Dendrocopos pubescens*)	+	+	–	F	I	P	B	D	24–48
Eastern Kingbird (*Tyrannus tyrannus*)	–	–	–	S	I	P	H	S	24–48
Great Crested Flycatcher (*Myiarchus crinitus*)	–	–	–	F	I	P	H	S	24–48
Eastern Phoebe (*Sayornis phoebe*)	–	+	+	S	I	P	L	S	12–24
Willow Flycatcher (*Empidonax traillii*)	–	–	–	S	I	P	H	S	12–24
Acadian Flycatcher (*Empidonax virescens*)	–	–	–	F	I	P	L	S	12–24
Eastern Wood Pewee (*Contopus virens*)	–	–	–	F	I	P	M	S	12–24

[a] L = length, D = depth, W = width of bill. [b] G = grassland, S = shrublands, F = forest. [c] O = omnivore, I = insectivore. [d] S = searcher, P = pursuer. [e] G = ground, B = bark, L, M, H = low, medium and high foliage. [f] G = glean, S = sally, D = drill.

APPENDIX 1– *Continued*

Species	Sexual Dimorphism[a] L	D	W	Habitat[b]	Food Habits[c]	Foraging Strategy[d]	Stratum[e]	Behavior[f]	Body Wt. Class (g)
Horned Lark (*Eremophila alpestris*)	+	–		G	O	S	G	G	24–48
Blue Jay (*Cyanocitta cristata*)	–	–	–	F	O	S	L	G	48–96
Tufted Titmouse (*Parus bicolor*)	–	–	+	F	I	S	M	G	12–24
Carolina Chickadee (*Parus carolinensis*)	+	+	–	F	I	S	M	G	6–12
Black-capped Chickadee (*Parus atricapillus*)	–	+	–	F	I	S	M	G	6–12
White-breasted Nuthatch (*Sitta carolinensis*)	–	–	–	F	I	S	B	G	12–24
House Wren (*Troglodytes aedon*)	–	–	–	F	I	S	L	G	6–12
Carolina Wren (*Thryothorus ludovicianus*)	+	+	–	F	I	S	L	G	12–24
Mockingbird (*Mimus polyglottos*)	–	–	–	S	O	S	G	G	48–96
Gray Catbird (*Dumetella carolinensis*)		–	–	S	I	S	L	G	24–48
Brown Thrasher (*Toxostoma rufum*)			–	S	O	S	G	G	48–96
American Robin (*Turdus migratorius*)	–	–	–	S	O	S	G	G	48–96
Wood Thrush (*Hylocichla mustelina*)	–	–	–	F	O	S	G	G	48–96
Eastern Bluebird (*Sialia sialis*)	–	+	+	S	O	P	L	G	24–48
Blue-gray Gnatcatcher (*Polioptila caerulea*)		–	–	F	I	S	H	G	3–6
Starling (*Sturnus vulgaris*)			–	F	O	S	G	G	48–96
White-eyed Vireo (*Vireo griseus*)	+	–	+	S	I	S	L	G	12–24
Bell's Vireo (*Vireo bellii*)	–	–	+	S	I	S	L	G	6–12
Yellow-throated Vireo (*Vireo flavifrons*)	+	+	+	F	I	S	H	G	12–24
Red-eyed Vireo (*Vireo olivaceus*)	–	–	–	F	I	S	H	G	12–24

APPENDIX 1—*Continued*

Species	Sexual Dimorphism[a]			Habitat[b]	Food Habits[c]	Foraging			Body Wt. Class (g)
	L	D	W			Strategy[d]	Stratum[e]	Behavior[f]	
Warbling Vireo (*Vireo gilvus*)	–	–	–	F	I	S	H	G	12–24
Prothonotary Warbler (*Protonotaria citrea*)	–	–	+	F	I	S	L	G	6–12
Blue-winged Warbler (*Vermivora pinus*)	–	–	–	S	I	S	H	G	6–12
Northern Parula (*Parula americana*)	–	–	–	F	I	S	H	G	6–12
Yellow Warbler (*Dendroica petechia*)	–	–	+	S	I	S	L	G	6–12
Cerulean Warbler (*Dendroica cerulea*)	–	–	–	F	I	S	H	G	6–12
Ovenbird (*Seiurus aurocupillus*)	–	–	–	F	I	S	H	G	12–24
Yellowthroat (*Geothlypis trichas*)	–	+	–	S	I	S	L	G	6–12
Yellow-breasted Chat (*Icteria virens*)	–	–	+	S	I	S	L	G	12–24
Kentucky Warbler (*Oporornis formosus*)	–	–	–	F	I	S	G	G	12–24
American Redstart (*Setophaga ruticilla*)	–	–	–	F	I	P	M	S	12–24
Eastern Meadowlark (*Sturnella magna*)	+	+	+	G	O	S	G	G	96–192
Red-winged Blackbird (*Agelaius phoeniceus*)	+	+	+	G	O	S	L	G	48–96
Common Grackle (*Quiscalus quiscula*)	+	+	+	S	O	S	G	G	96–192
Brown-head Cowbird (*Molothrus ater*)	+	+	+	S	O	S	M	G	24–48
Orchard Oriole (*Icterus spurius*)	+	+	–	S	I	S	H	G	12–24
Northern Oriole (*Icterus galbula*)	–	–	–	F	I	S	H	G	24–48
Scarlet Tanager (*Piranga olivacea*)	–	–	–	F	I	S	H	G	24–48
Cardinal (*Cardinalis cardinalis*)	–	+	–	S	O	S	L	G	24–48
Rose-breasted Grosbeak (*Pheucticus ludovicianus*)	–	–	–	F	O	S	H	G	24–48

APPENDIX 1—*Continued*

Species	Sexual Dimorphism[a] L	D	W	Habitat[b]	Food Habits[c]	Foraging Strategy[d]	Foraging Stratum[e]	Foraging Behavior[f]	Body Wt. Class (g)
Indigo Bunting (*Passerina cyanea*)	–	–	+	S	O	S	M	G	6–12
American Goldfinch (*Spinus tristis*)	–	–	–	S	O	S	L	G	12–24
Dickcissel (*Spiza americana*)	+	+	–	G	O	S	L	G	12–24
Rufous-sided Towhee (*Pipilo erythrophthalmus*)	–	–	–	S	O	S	G	G	24–48
Grasshopper Sparrow (*Ammodramus savannarum*)	–	–	–	G	O	S	L	G	12–24
Henslow's Sparrow (*Ammodramus henslowi*)	–	–	–	G	O	S	L	G	12–24
Vesper Sparrow (*Pooecetes gramineus*)	–	+	–	G	O	S	L	G	12–24
Field Sparrow (*Spizella pusilla*)	–	–	–	S	O	S	L	G	6–12
Song Sparrow (*Melospiza melodia*)			–	S	O	S	L	G	12–24

NEW LIFE MEMBER

Dr. William Yancey Brown has recently become a life member of the Wilson Ornithological Society. Dr. Brown received his Ph.D. from the University of Hawaii in 1973, and he is principally interested in sea bird ecology. His research interests and publications have been concerned primarily with the biology of Sooty Terns and Brown Noddies. He is a member of the AOU, Ecological Society of America, AAAS, and Sigma Xi. At the present Dr. Brown is a student at Harvard Law School.

BREEDING BALD EAGLES IN CAPTIVITY

JOHN R. MAESTRELLI AND STANLEY N. WIEMEYER

Large scale declines in some populations of Bald Eagles (*Haliaeetus leucocephalus*) in the contiguous United States have been documented by Broley (1958), Abbott (1967), and Sprunt et al. (1973). The percentage of pairs producing young and the average number of young produced annually per successful pair have been reduced in declining populations (Sprunt et al. 1973). Environmental pollutants have been implicated in the deaths of Bald Eagles (Reichel et al. 1969, Mulhern et al. 1970, Belisle et al. 1972) and in the reduced reproductive success of some populations (Wiemeyer et al. 1972).

To produce Bald Eagles for controlled studies dealing with non-reproductive effects of environmental pollutants, and to determine the requirements for breeding this species in captivity, a captive breeding project was initiated in the Section of Environmental Studies at the Patuxent Wildlife Research Center, Laurel, Maryland. Problems associated with captive propagation of raptors have been overcome for some species, but published accounts of Bald Eagles successfully breeding in captivity are rare. Hulce (1886, 1887, Bebe 1886) bred a pair of Bald Eagles in an enclosed porch beside his house in Ohio. His birds began producing fertile eggs in their sixth year and successfully raised three young over a two year period. A 14-year-old female Bald Eagle produced two young on her fourth attempt after being paired with three different males at the Buffalo Zoological Gardens (Anon. 1909, Herrick 1932b). A pair of Bald Eagles collected in Alaska during 1932-33 produced young on two occasions at the San Diego Zoo. Two young were raised in 1938 when the 6-year-old female and 5-year-old male bred in a large flight pen containing 30 additional species of raptorial birds (Hancock 1973). In 1953 the birds produced one young that lived for six days before being thrown from the nest (Anon. 1969). Barger (1963) reported that a pair of Bald Eagles at the Wisconsin Conservation Department's game farm at Poynette hatched two young in 1958: both died before 17 days of age.

Repeated breeding by a pair of White-tailed Sea Eagles (*Haliaeetus albicilla*) at the Vienna Zoo has been documented by Fiedler (1970). His birds produced at least one young per year from 1961 through 1969. The birds originally bred in a large flight pen containing various species of raptors but were moved to separate quarters after they killed two Bearded Vultures (*Gypaetus barbatus*) during their first breeding season.

Table 1

Measurements (mm) of Adult Female Northern and Southern Bald Eagles[1] Compared to a Captive Female

	Wing	Tail	Tarsus	Middle Toe
Southern Bald Eagle[3]	584–588[2]	247–286	101–107	66–77
	(576.5)	(271.2)	(103)	(71.8)
Northern Bald Eagle[4]	605–685	300–365	83–110	70–82
	(640.2)	(339.4)	(101.9)	(74.5)
Captive Female	568	271	99	70

[1] After Friedmann (1950).
[2] Extremes; means in parentheses.
[3] Eleven specimens from Georgia, Florida, Louisiana, and Baja California.
[4] Forty-two specimens from Bering Island, Alaska, Northwest Territories, New Brunswick, Maine, Massachusetts, New York, Pennsylvania, Virginia, Idaho, North Carolina (only wing length based on 42 specimens, other measurements based on 16 specimens).

We will here report on the successful breeding of a pair of captive Bald Eagles and present data on our husbandry methods.

METHODS AND MATERIALS

Source of Birds.—In January 1965, a female Bald Eagle (approximately 3 years old) was shipped to this center from Madison Co., Alabama where it was found with an injured wing beneath a high voltage line. After the wing healed, she was paired with a male taken from a nest near Juneau, Alaska in 1965 (at age 40 days) and exhibited at the National Zoological Park in Washington, D. C. until its transfer to Patuxent in 1968.

The size of the Bald Eagle gradually decreases from Alaska to Florida (Bent 1937) and is the basis for separating the birds into northern (*H. l. alascanus*) and southern (*H. l. leucocephalus*) subspecies (Friedmann 1950). Body measurements of our captive female indicate that she probably belongs to the southern race (Table 1). Bent (1937) states that the two Bald Eagle races intergrade extensively where their ranges overlap. Past records indicate that captive Bald Eagle breeding experiments were successful when birds with similar origins were paired together (Hancock 1973). The pronounced latitudinal difference in origin in our breeding eagles (58°N. Lat. versus 25–40°N. Lat.) indicates that formation of a pair bond may be as important to successful breeding as the pairs' origin.

The sex of our eagles was determined by cloacal examination and later confirmed by plasma steroid hormones (Dieter 1973).

Facilities.—The eagles were housed in the end cage of a row of eight flight pens located in a 3.2 ha fenced field surrounded by mixed stands of deciduous and pine (*Pinus virginiana*) trees. The flight pen floors and adjacent field were planted in *Lespedeza* sp. and left uncut during each breeding season. A row of smaller flight pens containing a colony of American Kestrels (*Falco sparverius*) faced the eagle pens. A one-story building near the flight pens originally contained offices, but was converted to a receiving warehouse for the Center in 1970. Because the end pen containing the

FIG. 1. Raptor flight pen containing a pair of breeding Bald Eagles. Pens in foreground house breeding American Kestrels.

breeding eagles faced the loading platform, canvas was placed on the end of the pen to minimize disturbance caused by the passage and unloading of trucks.

The pen of our breeding pair measured $22 \times 11 \times 5.5$ m high and had its long side in common with the adjacent pen (Fig. 1). Utility poles placed 1.5 m in the ground at 5.5 m intervals were used for the upright supports. Large beams supported the wire on the roof of the pens. The exterior sides and top of the pens were covered with 2.5×5 cm mesh weld wire. A double layer of poultry netting was used as a partition between adjacent pens. Hardware cloth, 91 cm wide, and buried 61 cm in the ground, surrounded the pens to prevent mammalian predators from burrowing into them. The hardware cloth overlapped the weld wire at ground level and was securely attached to it. Plywood sheets were nailed opposite the perch on the back and side wall for protection from the prevailing wind.

The pen contained a heated $61 \times 61 \times 10$ cm stainless steel water pan, a feeding stump for each bird, perches, and a nest platform. The nest platform was placed 3.7 m above the ground and was made of 1.2×1.2 m plywood supported by two beams attached to adjacent poles. A man-made nest, lined with pine bark mulch, was wired to the platform and was repaired before each nesting season. Sticks were placed on the ground to provide supplemental nest materials for the eagles.

To give the nest area some protection from the weather, three sheets of 1.2×2.4 m translucent fiberglass were attached to the roof over the nest platform. Hancock (1973) found that Bald Eagles nesting below the tree crown in British Columbia experienced a higher fledging rate than those nesting without an overhead cover. A plexiglass mirror, placed above the nest in December 1971, allowed the nest contents to be seen from outside the pen (Fig. 2). Following the 1972 breeding season, we modified the

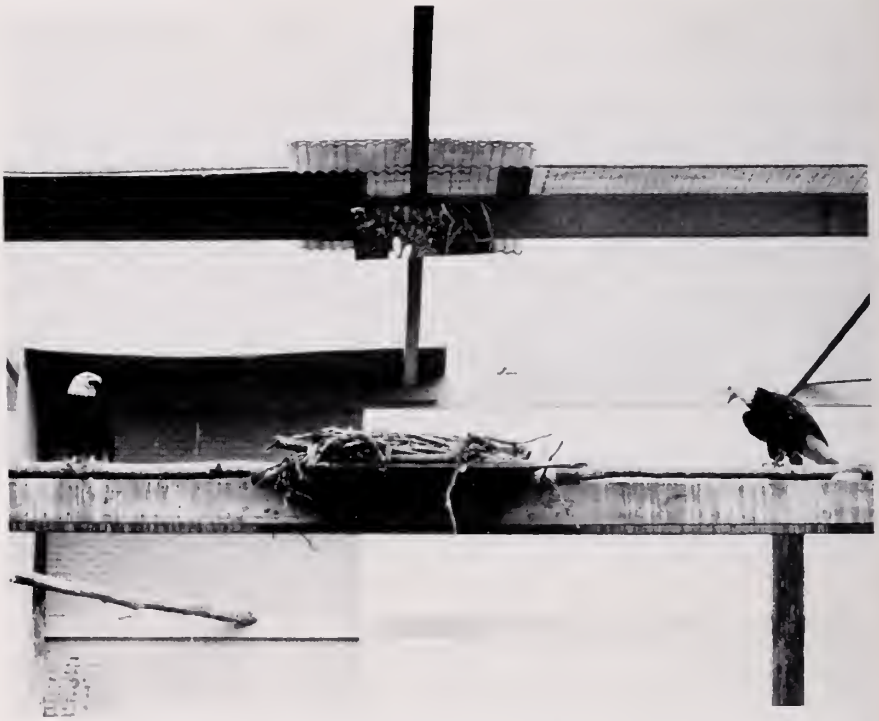

FIG. 2. Elevated nesting platform with three Bald Eagle eggs (visible in mirror above the nest).

eagle breeding pen by adding two additional sheets of fiberglass above the nest and fiberglass insulation beneath it.

Food.—During the breeding season the eagles were fed thawed whole animals once each morning; feeding was increased to twice a day after the eggs hatched and until the young fledged. Typical food included: laboratory rats, hamsters, guinea pigs, young chickens, and whole fish (both brackish and salt water species). During the non-breeding season the birds were fed once each morning 6-days a week. At that time, the diet consisted of whole animals or fish twice a week and one of two commercial foods (Zu-preem and Nebraska Brand Birds of Prey Diet) on the remaining days.

RESULTS AND DISCUSSION

In December 1969 three pairs of Bald Eagles were simultaneously placed in three of the completed pens: five pairs of Peregrine Falcons (*Falco peregrinus*) were placed in the remaining five pens. Following their placement in the flight pens, the eagles were usually examined once a year. Prior commitments during the 1970–72 breeding seasons precluded detailed obser-

vations. Extended observations were made with a 30× spotting scope during the 1973 season from an elevated blind about 120 m from the pens.

Behavior.—The breeding pair never was imprinted to humans even though the male was hand-raised as a nestling. During the non-breeding season, the eagles retreated at the approach of a person or vehicle. Following egg-laying and until the eggs or young were removed each year, the male attempted to attack anyone who approached the pen; the female often screamed from the nest perch.

Bald Eagles breeding in Florida tolerated crows (*Corvus* sp.) and vultures (Cathartidae) near the nest site (Howell 1937); Bald Eagles nesting in British Columbia ignored crows and Ospreys (*Pandion haliaetus*) unless they tried to perch in the nest tree (Retfalvi 1965). Herrick (1932a) reported that a female Bald Eagle brooding young rose quickly to her feet and raised her wings when a crow flew directly over the nest. On another occasion the male drove off a flock of crows early in the reproductive season when the first egg may have already been in the nest. In our study, crows, vultures, and an Osprey flying over the pen area during the breeding season elicited a series of high-pitched screams and rapid wing movements from the perched eagles.

Few instances of intraspecific conflict between eagles in adjacent pens were noted. On three occasions, a non-breeding eagle in an adjacent pen pen was frightened and flew along or into the partitioning wire where it was immediately attacked by one of the members of the breeding pair. These conflicts may have been kept at a minimum by having the perches and nest platform in the same position in each pen. No occurrences of strife were observed between members of our breeding pair.

The eagles added to their man-made nest by occasionally bringing a stick or more often, a tuft of dried grass to it prior to and following egg-laying.

Reproduction.—The breeding eagles may have had insufficient time to form a pair bond in the flight pen before the 1970 breeding season; also, this 5-year-old male may not have been sexually mature, which may explain why no reproductive activities were observed during that year.

In 1971, the pair was first seen incubating on 3 March. Following 56 days of incubation, we removed one whole egg and fragments of at least one other egg. No embryos were visible. In a review of captive Bald Eagle breeding projects, Hancock (1973) found that three of four pairs of mature birds that eventually hatched eggs produced infertile clutches during their first nesting attempt. The cause of infertile first clutches in captive eagles is unknown; field studies of known-age eagles are needed to determine if this commonly occurs among wild birds. Removal of the first clutch from captive eagles laying for the first time might stimulate renesting, although only a few

instances of wild eagles renesting following removal of their eggs have been recorded (Hoxie 1910, Herrick 1924, Bent 1937).

In 1972, the female began laying on 29 February and had deposited three eggs by 6 March. Incubation appeared to begin with the laying of the first egg. One egg hatched on 5 April and a second young appeared to be present on 8 April. An unseasonal ice storm on the night of 7 April left portions of the nest covered with ice. Both eaglets were dead by 10 April. On 19 April, we removed the remaining egg which contained an embryo that had died a a few days before hatching. The embryo plus the unabsorbed yolk weighed 64 g. less than that of an eaglet from Canada weighing 85 g at hatching (Herrick 1932b). Remains of the dead eaglets were not found. The adult eagles had brought food to the nest, but we are uncertain whether the young were fed. No further breeding attempts were observed that year. The female was found to be blind in the right eye prior to the 1973 breeding season.

On 16 January 1973, we observed the eagles bringing dried grass to the nest. The first egg was laid on 26 February. The pair copulated on a perch adjacent to the nest 2 days later. The female laid a second egg on 1 March; the third egg was first seen 4 days later.

Incubation on a regular basis did not begin until the second egg was laid. Both birds participated in incubation, as found by Herrick (1932a), with the female spending approximately twice as much time on the eggs as the male (N. Gerrard, pers. comm.). On three occasions just before dark the birds were observed sitting side by side on the nest in an incubating position for periods ranging up to 20 min (N. Gerrard, pers. comm.). Nicholson (1952) reported flushing both birds from two Florida nests after dark, but in his personal communication to Bent (1937) he stated that in both instances one bird was incubating or brooding while the other was perched near the nest.

A slight change in the normal incubation posture (back horizontal) was first noted on 2 April when the incubating eagle assumed a brooding posture in which its back sloped slightly toward its tail. Observations with the aid of the mirror on that date, during periods when the incubating adult was off the nest, indicated that pipping had not begun. The brooding posture became more pronounced on later days.

One egg was well pipped on 3 April; this egg probably hatched on 4 April. A second egg was pipped on 5 April and two young were present the next day. The third young hatched on 8 April after an incubation period of at least 34 days. Incubation periods reported for other studies include 34 to 35 days for wild Bald Eagles in Ohio (Herrick 1932a), 35 to 36 days for eagles in Florida (Nicholson 1952), and 35 to 37 days for a captive pair in Ohio (Hulce 1886, 1887).

Antagonism between the nestlings was apparent soon after hatching. Fighting was first observed the day after the second eaglet hatched and occurred when both adults were away from the nest. Two days later the young were again pecking at each other's head and, at one point, were grasping each other's beak. At that time, the parents were standing on the nest and offering food to the young. On 9 April one of our adult eagles picked up and partially ate what appeared to be a dead eaglet. Two young remained in the nest on the following day. Although the first two eaglets were most aggressive towards each other at about the time the third egg hatched, we don't know that the dead eaglet was the last to hatch or that its death was the result of fratricide.

Herrick (1932b) observed an older nestling attacking its younger nest mate; the younger nestling died at about 20 days of age. Dixon (1909) mentioned a case where the smallest of three nestling Bald Eagles being raised in captivity was killed by its nestmates. Ingram (1959) reported that fratricide is common among nestling eagles: he could not correlate the behavior with a lack of food. Gordon (1955) found that an older Golden Eagle (*Aquila chrysaetos*) nestling will repeatedly attack and often kill its younger nest mate.

Food placed in the pen after the young hatched was immediately picked up by the male and transferred to the nest. The actual feeding of the young was usually performed by the female. On 10 April, when the pair and their young were observed nearly continuously from 08:30 until 16:10, the young were fed three times at about 11:00, 12:50, and 14:30. Excess food items were often left on the nest.

The largest nestling was seen preening its down on 18 April when only 2 weeks old. The two nestlings were first seen standing in the nest on 29 May, and by 12 June were spending the day on perches connected to the nest, but returning to the nest to be fed. On 28 June, 85 days after the first eaglet hatched, we removed the fledged young from the high grass beneath the nest. Work being performed near the pens may have caused the young to prematurely fly from the nest, although Herrick (1924) found that two eaglets had left an Ohio nest after spending about 71 and 74 days in it. However, he computed the time spent in the nest after assuming the eaglets hatched following a 29-day incubation period rather than the normal 35- to 36-day period.

At fledging, the eagles weighed 3639 g and 4671 g, less than the average weights of 18 immature Bald Eagles collected in Alaska by Imler and Kalmbach (1955). They found an average weight of 4014 g for males and 5089 g for females. A captive-reared male Alaskan Bald Eagle weighed 4508 g at 74 days of age (Stewart 1970).

SUMMARY

A 7-year-old female Bald Eagle from Alabama was paired with a 4-year-old Alaskan male in a large flight pen during December 1969. Both birds were free of physical defects when originally placed in the pen but the female was blind in one eye prior to the 1973 breeding season.

Nesting first occurred during 1971 when at least two eggs were laid; all but one, which showed no sign of embryonic development after being incubated for 56 days, were broken by the adult birds. Two of three eggs laid in 1972 hatched. Both young died a few days after hatching following a period of inclement weather. Three eggs were laid and hatched during 1973. Antagonism between the nestlings was observed soon after hatching and may have been responsible for the unobserved death of one nestling, two days after the third young hatched. The two remaining young were raised by the adult birds and eventually left the nest 85 days after the first egg hatched. Incubation periods for the 1972–73 clutches averaged 35 days. No renesting attempts were made by the eagles during the 3-year period.

ACKNOWLEDGMENTS

We thank William Krantz for his help in designing the flight pens and James Rnos for his critical review of the manuscript. We also thank Naomi Gerrard for her detailed observations during part of the 1973 breeding season.

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U.S. FISH AND WILDLIFE SERVICE, SECTION OF ENVIRONMENTAL STUDIES, PATUXENT WILDLIFE RESEARCH CENTER, LAUREL, MD 20811 (PRESENT ADDRESS, JRM: U.S. FISH AND WILDLIFE SERVICE, FEDERAL BUILDING, 300 BOOTH ST., RM. 4007, RENO, NV 89502). ACCEPTED 15 JULY 1974.

REQUEST FOR INFORMATION

Least Terns.—As part of our research on the California Least Tern (*Sterna albifrons browni*), we are seeking information on (1) the location of breeding colonies in Baja California, Mexico, and (2) the migration routes and wintering areas of the subspecies. We would appreciate hearing of any Baja California observations of Least Terns, and of any records of Least Terns along the Pacific coast of Mexico, Central America, and South America from September through March. Please send your information to: Sanford R. Wilbur, U.S. Fish and Wildlife Service, 1190 E. Ojai Avenue, Ojai, CA 93023.

MOVEMENTS AND MORTALITY OF JUVENILE WHITE PELICANS FROM NORTH DAKOTA

Lawrence E. Strait and Norman F. Sloan

Nearly 8000 White Pelicans (*Pelecanus erythrorhynchos*) breed at Chase Lake National Wildlife Refuge, North Dakota (Lies and Behle, Condor 68:279–293, 1966; Sloan, Inl. Bird-Banding News 45:83–96, 1973), more than at any other locality in North America.

During 1972, we began banding young and studying juvenile mortality in order to define factors influencing the stability of the Chase Lake population. This paper reports on the movements and mortality of juvenile Chase Lake pelicans during their first fall migration.

METHODS

Band recovery data were made available by the Bird Banding Laboratory, Patuxent, Maryland. Only nestlings banded at Chase Lake National Wildlife Refuge (NWR) were considered in this analysis. Since 1928, pelicans have been banded at the refuge by Dr. Norman F. Sloan and co-workers from Michigan Technological University, Dr. and Mrs. Gammell of Kenmare, North Dakota, and personnel of the Arrowwood NWR, North Dakota.

Information supplemental to band recovery data was gathered by dyeing 193 nestlings in 1972 and 1973. We applied yellow picric acid dye, in a saturated alcohol solution, to the upper wings of young having fully developed covert feathers. Marking the coverts proved best because they are easily visible when the birds are on the water or standing on shore. Requests for sighting information on these marked birds were sent to state and federal conservation agencies.

LOCATION OF DISPERSAL

Recoveries of 306 pelicans banded as nestlings at the refuge were reported, out of approximately 10,000 young banded during the period 1928 to 1973 (Fig. 1). The period of juvenile dispersal extended from August through the following January. Generally, juveniles moved from central North Dakota (location of the Chase Lake Refuge) south to the Gulf Coast, and subsequently east to Florida and south into Mexico and Central America. A concentration of recoveries occurred in the area between central Minnesota and the Missouri River in North and South Dakota. From this region south to the Gulf Coast recoveries were more widely scattered in a 300 km wide corridor lying west of the Mississippi River. Northward movement during this dispersal period was not indicated in the band recoveries.

Along the Gulf Coast pelicans still tended to remain west of the Mississippi River. Only 15 bands were recovered east of the Mississippi, while 38 were

FIG. 1. Each dot represents the U.S. recovery location of a Chase Lake White Pelican during its first fall migration.

recovered along the Texas and Louisiana coasts and 78 were recovered from 15 Mexican states, Salvador, and Nicaragua. The Mexican recoveries were concentrated in the eastern Gulf Coast states of Tamaulipas and Vera Cruz.

TIMING OF DISPERSAL

The first color-marked young reported away from Chase Lake was on 27 August 1973, at Tewaukon NWR in southeastern North Dakota (Table 1). Reports in North and South Dakota occurred primarily in September: the latest for South Dakota was 18 October. On 21 September 1972, some color-marked young were still present at Chase Lake, but on the same date a marked bird was reported from Nebraska. Most healthy young leave North

Table 1

Observations of color-marked White Pelicans outside Chase Lake National Wildlife Refuge in 1972 and 1973

Date	Number of Marked Young	Location	Estimated Number of White Pelicans in Area
27 Aug. '73	1	Tewaukin NWR, ND	500
24–31 Aug. '73	2	Tewaukin NWR, ND	100
30 Aug. '73	2	near Woodworth, ND	10
31 Aug. '73	10	near Woodworth, ND	30
6 Sept. '73	1	Squaw Creek NWR, MO	62
6 Sept. '73	1	Chokio Game Mgt. Area, MN	80
7 Sept. '73	1	Wessington Springs, SD	—
8 Sept. '73	5	Cheyenne Bottoms WMA[1], KS	—
12 Sept. '73	1	Lake Andes NWR, SD	2500
12 Sept. '73	2	Lake Byron, Beadle Co., SD	375–400
15 Sept. '73	4	Cheyenne Bottoms WMA, KS	10,000–12,000
16 Sept. '73	1	Crescent Lake NWR, NB	100
17 Sept. '72	1	Brant Lake, Lake Co., SD	Flock
18 Sept. '73	3	Cheyenne Bottoms WMA, KS	6000–8000
19 Sept. '72	1	Philbrick Lake, Brown Co., NB	46
2–3 Oct. '73	2	Marion Res., near Hillsboro, KS	—
21–24 Sept. '72	1	Philbrick Lake, Brown Co., NB	1
21 Sept. '72	1	Long Lake, Brown Co., NB	Flock
24 Sept. '72	1	Cheyenne Bottoms WMA, KS	Many
26 Sept. '72	1	Cheyenne Bottoms WMA, KS	Flock
26 Sept. '72	2	Crystal Lake, near Plankinton, SD	500
26 Sept. '72	1	Chelsea, SD	1
4 Oct. '72	1	Blue Dog Lake, near Waubay, SD	—
6 Oct. '73	1	Harlan County Res., near Alma, NB	—
6 Oct. '72	1	Crescent Lake NWR, NB	7
8 Oct. '72	1	Harvard Marsh Lagoon, near Hastings, NB	1
9 Oct. '73	10	Rockefeller Refuge, LA	8000
10–18 Oct. '72	1	Lake Madison, near Madison, SD	1
11 Oct. '72	1	Pratt County Lake, KS	1
11 Oct. '72	1	Biloxi Bay, Ocean Springs, MS	30
12 Oct. '72	1	Quivera NWR, KS	1100
12 Oct. '72	1	Squaw Creek NWR, MO	60
15 Oct. '72	1	Cheyenne Bottoms WMA, KS	10
15 Oct. '72	1	Cheyenne Bottoms WMA, KS	400
16 Oct. '72	1	Quivera NWR, KS	1000
18 Oct. '72	1	Neosho WMA, KS	4
18 Oct. '72	1	Salt Plains NWR, OK	100
20 Oct. '72	1	Cheyenne Bottoms WMA, KS	—
20 Oct. '73	1	Fish Lake, Deuel Co., SD	1
22 Oct. '72	1	Cheyenne Bottoms WMA, KS	—

[1] WMA = Wildlife Management Area.

TABLE 1 (continued)

Date	Number of Marked Young	Location	Estimated Number of White Pelicans in Area
24 Oct. '72	1	Kirwin NWR, KS	1
24 Oct. '73	2	Rockefeller Refuge, LA	300–500
25 Oct. '72	1	Kirwin NWR, KS	18
27 Oct. '72	1	Quivera NWR, KS	200
9 Nov. '73	3	Ouachita River near Monroe, LA	100
16 Nov. '73	1	Sequoyah NWR, OK	48
20 Nov. '72	1	Salt Plains NWR, OK	17
16 Jan. '73	5	Laguna Atascosa and Santa Ana NWR's, TX	80

Dakota by mid-September. Sightings in Kansas occurred from 8 September through 22 October. Peak numbers of 10,000 to 12,000 birds were reported at Cheyenne Bottoms on 15 September 1973. By late October, the bulk of the population had left Kansas. The latest observation of a young bird north of the Gulf Coast occurred 20 November 1972, at Great Salt Plains Reservoir, Oklahoma.

The behavior of marked young was noted by several observers. They were usually observed in flocks ranging in size from four to 8000 birds. Juveniles occurring singly were frequently reported by observers as appearing sick. One observer thought a marked bird was ostracized by the flock, but another reported a marked young leading a flock of pelicans in "V" formation. No dyed pelicans were reported in the spring: the dye must have worn off or the coverts were molted over the winter.

MORTALITY

Shooting was the cause of death for 27.8% of banded birds reported (Table 2). This included 13.1% of all U.S. recoveries and 71.1% of Mexican and Central American recoveries. Kansas and Iowa were the only two states in the U.S. where more birds were reported as "shot" than "found dead." In North Dakota no birds were reported "shot." Birds "found dead" account for 46.7% of the total recoveries. Other causes of death frequently reported were injury, 4.6%; disease, 4.6%; and entanglement in fishing gear, traps, or snares, 2.0%.

CONCLUSIONS

During the fall migration, White Pelicans make major use of federal and state management areas. Tewaukon NWR in North Dakota, Lake Andes

Table 2

Nature of Recoveries by State of Chase Lake White Pelicans Banded as Nestlings, 1928–1972

State	Found Dead	Shot	Caught Due to Injury	Caught Due to Disease	Caught In Trap, etc.	Flight Accident	Caught By Hand	Band or No. Only	Misc.	Total
Texas	26	6	2	2	3	1		2		42
S. Dakota	23	3	4	4			1		1	36
Vera Cruz	3	20					2	2		27
N. Dakota	16		1	2			3		1	23
Kansas	8	9				1	1	2	1	22
Missouri	9	2	3	1	1			1		17
Louisiana	10	1	1	1	1			1	1	16
Tamaulipas	2	11			1			2		16
Oklahoma	7	2				1	1	3		14
Minnesota	10	2	1							13
Florida	9			1				1		11
Nebraska	5	1	1				2	1	1	11
Arkansas	5	1						1	2	9
Chiapas		5					1			6
Iowa	1	3					2			6
Oaxaca		5								5
Alabama	2		1	1						4
S. L. Potosi	1	2						1		4
Campeche		3								3
Mississippi	3									3
Coahuila		1						1		2
Guerrero	1	1								2
Jalisco		1							1	2
Salvador	1	1								2
Tabasco		1		1						2
Tuxtilla		1						1		2
Chihuahua		1								1
Mexico		1								1
Michoacan								1		1
Nayarit		1								1
Nicaragua								1		1
Tennessee	1									1
Total	143	85	14	13	6	3	13	21	8	306
Percent	46.7	27.8	4.6	4.2	2.0	1.0	4.2	6.9	2.6	100

NWR in South Dakota, Quivera NWR, Cheyenne Bottoms Wildlife Management Area in Kansas, and Rockefeller Refuge in Louisiana have been concentration points in recent years for the Chase Lake flock. These areas provide feeding and loafing areas for a large percentage of the central North American population, currently estimated at 34,000 birds (Sloan, Inl. Bird-Banding News 45:83–96, 1973).

Shooting is the largest single known cause of mortality. The White Pelican was included under the Migratory Bird Treaty in 1972; thus only recently has it been given protection. First-year Chase Lake pelicans move

to the Gulf Coast during the period from late August through most of November. They are exposed to fall waterfowl hunters during much of this movement. The refuge manager at LaCreek NWR reported that some pelicans are shot every year when mistaken for Snow Geese, *Chen caerulescens*. This problem will remain until hunters learn to distinguish the two species.

Shooting losses appear much greater in Mexico and Central America than in the U.S. Diem and Condon (Yellowstone Library and Museum Association Bulletin, 1967) suggested that persons shooting pelicans in Mexico turn in bands readily expecting a reward and that Mexican figures for birds shot may be a better indication of numbers of pelicans shot in the U.S. than band returns indicate. In the U.S. persons often report banded birds they have shot as found dead or not at all because they fear being penalized for shooting such a bird.

ACKNOWLEDGMENTS

We wish to express appreciation for financial support of this study by the Max McGraw Wildlife Foundation, and The Foundation For Environmental Education. Also the support furnished by personnel of the Arrowhead National Wildlife Refuge and the Northern Prairie Wildlife Research Station, Jamestown, North Dakota and especially the substation at Woodworth, North Dakota is acknowledged. We wish to thank all of those who reported sightings of color-marked birds.

DEPT. OF FORESTRY, MICHIGAN TECHNOLOGICAL UNIV., HOUGHTON MI 49931.
ACCEPTED 1 NOV. 1974.

NEW LIFE MEMBER

Mr. Robert E. Ball is now a life member of the Wilson Ornithological Society. Mr. Ball is Secretary and Assistant Vice President of the First Federal Savings and Loan in Canton, Ohio. He has had a life long interest in bird study with special interest in migration and bird songs. He has published a number of popular articles including two in The Home Garden magazine. Mr. Ball is a life member of the AOU, a charter member of Hawk Mountain Sanctuary Association, a long time member of Cornell Laboratory of Ornithology, the Federation of Ontario Naturalists and the Federation of New York State Bird Clubs, Inc. Besides bird study, Mr. Ball is interested in photography and horticulture, and he has the unusual hobby of collecting wind-up toys.

CLAM DROPPING BEHAVIOR OF THE GLAUCOUS-WINGED GULL (*LARUS GLAUCESCENS*)

David P. Barash, Patrick Donovan and Rinda Myrick

Tinbergen (1961) and Oldham (1930) have reported that Herring Gulls (*Larus argentatus*) commonly drop whelks (*Baccinum undatum*) and other hard-shelled molluscs in order to break them open, but that their selection of substrate appears to be random, with the birds as likely to drop potential food objects on soft surfaces (sand) as on hard (rocks). The European Gull (*Larus canus*) also shows this same apparently non-adaptive behavior with regard to cockles (*Cardium edule*, Oldham 1930). This curious failure of such adaptive food generalists to make maximal use of a foraging technique is surprising. Our own observations of Glaucous-winged Gulls (*Larus glaucescens*) in northwestern Washington suggested that this species also commonly feeds on marine shellfish, which it opens by dropping. We therefore attempted to investigate substrate selection and other behaviors related to this clam dropping habit.

METHODS AND RESULTS

We conducted this study on Center Island, one of the San Juan Islands, and at Golden Gardens Park, Washington, between 5 November 1973 and 22 May 1974. Results for the two study areas were comparable and are combined for the following report. A large population of Glaucous-winged Gulls was commonly present. Although it was not possible to recognize most individuals, 3 adults and 3 two-year-olds were identified by feather peculiarities. In addition, 4 adults and 2 yearlings were live-trapped and marked with distinctive dye patterns. Both areas contained a variety of substrates: rock, cement, wood, sand, and water. A minimum of 20 m^2 of each substrate was present within ¼ km of each study site. During each set of observations, a small pile of 3–15 butter clams (*Sacidonus giganteus*) was exposed to the gulls, and detailed records were made of their feeding behavior. The substrate upon which the clams were placed was determined each time by use of a random numbers table, so as not to consistently predispose subsequent behavior toward any particular substrate.

The gulls used either standing or flying drops to open the clams. During standing drops the clams were released while the gull remained on the ground. There was considerable variation in this behavior, especially with regard to the position of the head when the clam was released. Head position during standing drops varied from maximum vertical extension to just a few

TABLE 1

SUBSTRATES UPON WHICH CLAMS WERE DROPPED

	Rock	Wood	Cement	Sand	Water	Total
Flying Drops	79	38	12	11	6	146
Standing Drops	420	159	21	20	0	620
Totals	499	197	33	31	6	766

centimeters above the substrate. With successive standing drops there was often an incremental lowering of the head until the clam appeared to be deposited almost directly upon the substrate. Flying drops occurred at altitudes ranging from 0.5 to 15 m and appeared to be most commonly 4 to 7 m. They characteristically involved a horizontal flight of varying length followed by a brief, almost vertical ascent, a hover of about 0.5 sec, and then the drop itself. The substrates upon which all observed clams were dropped are presented in Table 1.

Combining rock, wood, and cement as "hard" substrates as opposed to the "soft" substrates of sand and water, gulls used the former significantly more often (binomial test: Siegel 1956, $p < .001$). Standing drops were also used significantly more often than were flying drops ($p < .001$). Although this trend is apparent for both hard and soft substrates, the preference for standing drops appears greater on the hard substrates (82% standing vs 18% flying) than on the soft ones (54% standing vs 46% flying); however, because of the small number of soft-substrate drops, this possible trend cannot reliably be evaluated.

Predictably, flying drops are more effective than standing drops: the former averaged 1.72 drops per clam (SD .63) the latter, 3.91 (SD 1.19). The difference is significant (t-test, $p < .001$). Similarly, hard-substrate drops are more effective than their soft counterparts: hard substrate flying drops were always successful the first time (one drop per clam), while soft-substrate flying drops averaged 1.96 (SD .70: t-test, $p < .01$). Hard-substrate standing drops averaged 2.54 drops per clam (SD .48), while soft-substrate standing drops averaged 4.23 (SD .69: t-test, $p < .01$).

We also attempted to identify the factors involved in the selection of dropping techniques, standing vs flying. Time of day, height of the tide and age of the animals provided no significant correlations. However, the technique employed was correlated with the abundance of gulls in the immediate area. We estimated the gull density within 50 m of the clam-dropping animal on 80 arbitrarily selected observations: flying drops averaged 11.6 animals

within 50 m (SD 7.3) and standing drops averaged 26.4 (SD 10.9). These data produced a point biserial correlation coefficient of 0.31 (Walker and Lev 1953), indicating a significant ($p < .01$) correlation of flying drops with low density of nearby animals and of standing drops with high density.

Clearly, gulls do not drop all prospective food items: a simple experiment investigated the cues involved. Soft clay models of butter clams were interspersed with the real ones on five occasions: the models were probed with the bill but never dropped. Kiln-hardened models, however, were dropped and treated the same as real clams, suggesting that hardness, perhaps combined with visual properties, identifies the object as one worthy of being dropped.

Our observations also indicate an age-related progression of increased clam-slamming efficiency in this species. Thus, yearling gulls accounted for 6% of the 729 hard-substrate drops, and 78% of the 37 soft-substrate drops ($p < .01$). Two-year-olds accounted for 13% of the hard-substrate drops and 14% of the soft-substrate drops, while adults performed 81% of the hard-substrate drops and only 8% of the soft ($p < .01$). In addition to substrate selection, learning may also be reflected in the actual techniques of clam dropping, both standing and flying. Thus, yearlings fumbled their clams (dropping them when attempting to fly) on 29% of their attempts: this occurred in only 7% of adult attempts. Furthermore, yearlings accounted for all of the flying drops made from less than 1 m (9) and greater than 10 m (11). The unusually low-altitude drops appeared to be less successful than those in the more normal range and probably constitute inefficient use of the energy expended in performing a flying drop. Correspondingly, 6 (55%) of the very high altitude drops resulted in the clam being appropriated by other gulls before the original bombardier was able to descend. By contrast, only 8% of normal altitude drops were consumed by animals other than the one performing the drop.

Yearlings also appeared to be less efficient at standing drops. Thus, they accounted for 64% (111 of 174) of the standing drops estimated to have been less than 10 cm as opposed to 22% (98 of 446) of those exceeding 10 cm in height. The biserial correlation coefficient relating height of standing drops (above or below 10 cm) with number of drops required was .36, indicating that greater height required significantly fewer drops ($p < .05$). On the other hand there was no suggestion that the choice of clam dropping technique (standing vs flying) correlated with age. Dichotomizing the data into adults vs juveniles and standing vs flying drops produced a tetrachoric correlation coefficient of .13 (Walker and Lev 1953) indicating no significant correlations.

Finally, certain dropping sites appeared to be preferred by certain indi-

viduals and in some cases, even partially defended. Four individually recognized adults each used different rock areas during a two-month period for all their flying drops and 63% of their standing drops. There was no discernible tendency for juveniles to similarly concentrate their activities at particular places. On seven occasions a juvenile flying with a clam was chased away from one of these rock areas by the adult proprietor. No adults with clams were seen to intrude onto these four areas; however, when they were not carrying clams, both adults and juveniles often congregated on these rocks and were not attacked.

DISCUSSION

Flying drops are more efficient in terms of the number of such drops required for success but presumably are more expensive metabolically than are standing drops and also carry a greater risk of the food being pirated by other animals. The precise circumstances that render one strategy more efficient than the other are not known, but local density of potential competitors may be important, with lower density favoring flying drops and higher density favoring standing drops. In either case, use of a hard substrate seems maximally efficient.

As suggested by the relative inefficiency of juveniles, clam dropping behavior may well involve learning. The relatively well-developed flying ability of juveniles strongly suggests that the disparity between their performance and that of adults is not caused by maturational factors. However, this situation could be clarified by observations of newly-released captive animals who had been deprived of the opportunity to feed in this manner. In addition, further field studies in other geographic regions may be worthwhile in determining the extent to which clam dropping is a locally learned tradition, possibly analogous to other food-gathering techniques already documented for birds (Hinde and Fisher 1952) and primates (Itani 1958).

Brown (1964) has emphasized that territorial behavior requires resources that are economically defensible. Rocks that are particularly suitable for breaking clams would appear to fall within this category. If clam dropping rocks are selectively defended only against gulls that are themselves carrying clams, this would introduce a novel aspect to the literature on territorial behavior. We might expect that such defense is actually somewhat nonadaptive, since the resource itself (the rocks) is not diminished by another animals' use, and indeed, the proprietor may benefit by frequent use of his property assuming that he occasionally can pirate a clam dropped by another bird. In this sense, his apparent defense may simply represent an aggressive attempt to steal the clam from another bird, behavior which may be more likely for an animal whose social dominance is enhanced by proximity to a

familiar area. On the other hand, defense of a suitable clam dropping area may itself be adaptive if it reduces the local population density around these rocks, thereby decreasing the probability that the proprietor will himself suffer piracy when breaking open his own clams.

In the present study, juveniles were never seen to defend any clam dropping area and their generally reduced use of hard over soft substrates may reflect their lower social status as much as inadequate learning. Thus, juvenile Glaucous-winged Gulls feeding on spawned salmon in Alaska are relegated to less desirable feeding areas (Moyle 1966).

Finally, it remains to be pointed out that the Greek poet, Aeschylus, is reputed to have been killed by a falling tortoise that had been dropped onto his (hard substrate) bald head by a passing bird. Although the culprit species remains unidentified, the present study suggests that further investigation of clam-dropping behavior in gulls may be a hazardous activity, especially for ornithologists with receding hairlines!

SUMMARY

Glaucous-winged Gulls break open clams by dropping them, using either standing or flying drops. Both techniques preferentially utilize hard substrates, in distinction to previous reports for several European species. The relative efficiency of hard vs soft substrates, and high vs low standing and flying drops was investigated. Adults are more efficient clam droppers than are juveniles, and certain clam dropping areas may be actively defended.

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HABITAT ORDINATION OF PASSERINE BIRDS OF THE VIRGIN RIVER VALLEY, SOUTHWESTERN UTAH

Robert C. Whitmore

During the past 20 years much attention has been placed on defining habitat preferences of bird species and habitat differences between or among species. Focus has been both on closely related species groups (Sibley 1954, Dilger 1956, MacArthur 1958, Selander 1964) and entire communities (Bond 1957, Beals 1960, Cody 1968, James 1971). The theory that individual animals seek out a certain spot in the environment based on specific search images, early experience, genetic make-up or a combination of these factors is widely discussed in the literature (see Klopfer 1963, 1970). The environmental configuration of the selected sites has been termed the "niche gestalt" by James (1971). It has also been demonstrated, both theoretically and quantitatively in the field, that no two species can occupy the same niche for any prolonged period of time (Gause 1934, Hutchinson 1959, MacArthur 1968, 1970). It is the purpose of this study to determine quantitatively the spatial configuration of a group of passerine birds in their environment through the use of an ordination technique, to determine which habitat variables are most responsible for the separation of the species and to compare these results with those of a similar study (James 1971).

DATA COLLECTION AND METHODS OF ANALYSIS

Data were collected between 1 May and 30 June 1973, in the Virgin River Valley of southwestern Utah. The study area included the Santa Clara Creek from the Shivwits Indian Reservation to its junction with the Virgin River, along the Virgin River to Zion National Park and parts of Ash Creek at its junction with the Virgin River. The area is characterized by stands of dense tamarix (*Tamarix pentandra*), large clumps of mature Fremont cottonwood (*Populus fremontii*) and scattered patches of sand bar willow (*Salix exigua*). Much of the river valley is planted with alfalfa. In isolated marsh areas bull rush (*Scirpus americanus*), cattail (*Typha* sp.) and similar species may be found.

I collected data in a manner similar to that of James and Shugart (1970) using a modification of the range finder circle method. Data were collected from 0.1-acre (0.04-ha) circular plots with a singing territorial male bird as the center of the circle. The biases of this type of sampling are discussed elsewhere (James 1971) and are not considered important here. The variables measured for each plot are listed in Table 1. Percent canopy cover, percent ground cover and percent shrub density were all measured by taking about 20 sightings along transects from the center of the territory to its periphery, a distance of 11.3 m. Trees were divided into five 3 inch (7.62 cm) size classes and were measured directly at breast height using a graduated stick held at arms length. Tree species was also recorded. I measured canopy height using the modified Boy Scout method which uses a mirror held perpendicular to the tree, parallel

Table 1

Summary of the Variables Entered by the Discriminant Function Program and their Respective F-Values

Step	Variable Entered	F-Value
1	Percent Canopy Cover	53.99
2	Percent Shrub Density	21.82
3	Number of Trees 3–6 inches (7.62–15.24 cm) DBH	19.18
4	Percent Ground Cover	17.86
5	Number of Trees 6–9 inches (15.24–22.86 cm) DBH	6.74
6	Number of Trees > 15 inches (38.1 cm) DBH	7.11
7	Number of Trees 9–12 inches (22.86–30.40 cm) DBH	4.52
8	Canopy Height in feet (meters)	4.14
9	Number of Trees 12–15 inches (30.4–38.1 cm) DBH	3.80
10	Number of Species of Trees	1.92

to the ground. Upon approaching the tree with the hand held mirror outstretched, the point where the crown of the tree first appears is marked and the distance from the point to the tree plus 3 feet (0.91 m) is the estimated height of the tree. A total of 421 samples was taken for 24 species of passerine birds (Table 2).

I subjected the data to stepwise discriminant function analysis, a multivariate statistical technique. Lately multivariate analysis has been used as a tool to analyze the spatial configuration of organisms in the environment and to determine which variables are important in their separation (Cody 1968, James 1971, Green 1971, 1974).

Summarizing the discussion of discriminant function analysis from Sokal and Rohlf (1969) will give the basic ideas behind this statistical tool. Supposing habitat relationships for two different species of birds are desired and several characters, x_1, x_2, x_3 . . . . are measured for each one. Although the means of x_1 for the two species are dissimilar, they may not be sufficiently different to distinguish significantly between the two species. The same is true for the second and third characters and so on. Discriminant function analysis computes a new variable, Z, which is a linear function of the measured variables. The function is of the type

$$Z = a_1x_1 + a_2x_2 + a_3x_3 \ldots$$

which is the equation of a line cutting across the intermixed cluster of points representing the two species. This function is constructed in such a way that as many as possible of the members of one population have high values of Z and as many as possible of the members of the other have low values, so that Z serves as a much better discriminant of the two populations than do each of the measured variables taken separately. The assumptions for the valid use of discriminant analysis are discussed by Green (1971) and are considered to be met in this study. My data were analyzed using the BMD-07M stepwise discriminant analysis computer program (Dixon 1967). The program also computes F statistics between pairs of species based on the variables measured.

RESULTS AND DISCUSSION

The importance of the individual habitat characteristics as predictors of which bird species will occupy a particular environment is summarized in Table 1. This table is based on Bargman's extension of the discriminant analysis program which computes the relative importance of variables in their ability to distinguish between populations. All 10 variables (Table 1) contribute to the separation of the species although the contributions of the first four are considerably greater than the others. The most important variable, percent canopy cover, has been found to be of principal importance in several previous studies (see James 1971) and, therefore, its rank as number one is not surprising. The placement of shrub density as the second most important variable and the number of trees 3–6 inches (7.62–15.24 cm) diameter breast height as the third most important variable is of interest. These characteristics reflect the scattered stands of cottonwoods, separated by dense tamarix and young willows in my study area. Different bird species occur in these two types of habitat within the area and this results in the importance of these two variables as separating devices.

The alfalfa grown on the farms surrounding the rivers also affects the bird species present. Many species which actively defend territories in the riparian community often forage for food in the fields surrounding it. As a result their defended territories are in the periphery of the streamside vegetation and often contain part of the cropland. This causes percent ground cover to be an important variable for species separation.

Two variables of minor importance here, the number of tree species and the canopy height, were of major importance in the study by Frances James (1971). This is, however, not a discrepancy in the study methods nor techniques but a reflection of geographic differences. James worked in the deciduous forest of Arkansas where many species of trees with differing heights are likely to be found in any one sample, whereas my study is essentially restricted to two species of trees, each of similar height. The homogeneity of height in my study area is due, in part, to the extreme intolerance to shade of *Populus fremontii*, making growth of young trees difficult in mature stands. The difference in variable importance between the Utah and Arkansas study areas demonstrates a principle of this particular method of analysis in that the importance of variables is determined by the nature of the environment and should likely change from one area to the next.

Figure 1 presents a linear arrangement or ordination of the bird species along the first discriminant axis. High values on this axis indicate more heavily forested areas whereas low values indicate more open areas with higher ground cover.

Table 2

A Comparison of the James (1971) and Whitmore Ordinations on the First Discriminant Axis[1]

Arkansas James Ordination		Utah Whitmore Ordination	
3.2	Prairie Warbler (*Dendroica discolor*)	1.80	Blue Grosbeak (*Guiraca caerulea*)*
5.6	Bell's Vireo (*Vireo bellii*)	2.20	Indigo Bunting (*Passerina cyanea*)*
6.5	Brown Thrasher (*Toxostoma rufum*)	2.57	Western Kingbird (*Tyrannus verticalis*)
6.7	Yellowthroat (*Geothlypis trichas*)*	2.91	Lazuli Bunting (*Passerina amoena*)
8.0	Field Sparrow (*Spizella pusilla*)	2.97	Red-winged Blackbird (*Agelaius phoeniceus*)
8.1	Blue Grosbeak (*Guiraca caerulea*)*	3.07	Abert's Towhee (*Pipilo aberti*)
8.3	Eastern Kingbird (*Tyrannus tyrannus*)	3.17	House Wren (*Troglodytes aedon*)
8.8	Chat (*Icteria virens*)*	3.28	Willow Flycatcher (*Empidonax traillii*)
9.0	Chipping Sparrow (*Spizella passerina*)	3.54	Ash-throated Flycatcher (*Myiarchus cinerascens*)
12.9	Rufous-sided Towhee (*Pipilo erythrophthalmus*)	3.94	Chat (*Icteria virens*)*
14.2	Orchard Oriole (*Icterus spurius*)	4.34	Song Sparrow (*Melospiza melodia*)
15.4	Indigo Bunting (*Passerina cyanea*)	4.63	Yellowthroat (*Geothlypis trichas*)*
19.8	Robin (*Turdus migratorius*)	4.89	Bewick's Wren (*Thryomanes bewickii*)
22.3	Common Grackle (*Quiscalus quiscula*)	4.91	Bullock's Oriole (*Icterus galbula bullockii*)*
25.4	Cardinal (*Cardinalis cardinalis*)	5.01	Lucy's Warbler (*Vermivora luciae*)
25.6	Red-headed Woodpecker (*Melanerpes erythrocephalus*)	5.20	Blue-gray Gnatcatcher (*Polioptila caerulea*)*
25.9	Catbird (*Dumetella carolinensis*)	5.30	MacGillivray's Warbler (*Oporornis tolmiei*)
26.1	Kentucky Warbler (*Oporornis formosus*)	6.04	Black-headed Grosbeak (*Pheucticus melanocephalus*)
26.2	Blue-gray Gnatcatcher (*Polioptila caerulea*)*	6.79	Lesser Goldfinch (*Spinus psaltria*)
27.0	Brown-headed Cowbird (*Molothrus ater*)*		
28.9	Red-bellied Woodpecker (*Centurus carolinus*)		
29.6	Louisiana Waterthrush (*Seiurus motacilla*)		
30.0	Baltimore Oriole (*Icterus galbula galbula*)*		
31.6	Blue Jay (*Cyanocitta cristata*)		
32.2	Warbling Vireo (*Vireo gilvus*)*		
32.4	Prothonotary Warbler (*Protonotaria citrea*)		
32.7	White-eyed Vireo (*Vireo griseus*)		
34.3	Carolina Chickadee (*Parus carolinensis*)		
34.4	American Redstart (*Setophaga ruticilla*)		
36.4	Yellow-billed Cuckoo (*Coccyzus americanus*)		
36.6	Crested Flycatcher (*Myiarchus crinitus*)		
36.8	Eastern Wood Pewee (*Contopus virens*)		

[1] The scales of the ordinations are not the same due to different transformations of the data but increasing values represent habitats of increasing biomass in both studies. Species marked with an asterisk are found in both ordinations.

TABLE 2 (continued)

Arkansas James Ordination		Utah Whitmore Ordination	
38.7	Scarlet Tanager (*Piranga olivacea*)	7.02	Warbling Vireo (*Vireo gilvus*)*
39.0	Hooded Warbler (*Wilsonia citrina*)	7.30	Brown-headed Cowbird (*Molothrus ater*)*
39.1	Tufted Titmouse (*Parus bicolor*)	7.68	Wilson's Warbler (*Wilsonia pusilla*)
39.5	Downy Woodpecker (*Dendrocopos pubescens*)	9.01	Yellow Warbler (*Dendroica petechia*)
39.8	Black and White Warbler (*Mniotila varia*)	9.57	Audubon's Warbler (*Dendroica coronata auduboni*)
40.1	Yellow-throated Vireo (*Vireo flavifrons*)		
40.9	White-breasted Nuthatch (*Sitta carolinensis*)		
41.5	Parula Warbler (*Parula americana*)		
41.7	Wood Thrush (*Hylocichla mustelina*)		
41.8	Ovenbird (*Seiurus aurocapillus*)		
43.0	Carolina Wren (*Thryothorus ludovicianus*)		
43.2	Red-eyed Vireo (*Vireo olivaceus*)		
43.3	Acadian Flycatcher (*Empidonax virescens*)		

A two-dimensional plot of the first and second discriminant axes is presented in Figure 2. The same generalizations hold true for the first axis here as in Figure 1. The second axis represents variation in shrub density. For example, the Bullock's Oriole lies midway on the first axis indicating moderate values of ground cover, and total number of trees, but it lies at the upper end of the second axis indicating an extremely low shrub density value. At the other extreme the Willow Flycatcher lies in the area of high shrub density on the second axis and in the area of moderate numbers of trees on the first axis.

Interesting comparisons can be made among the eight species of birds ordinated along the first discriminant axis both here and in the study by James (see Figs. 1 and 2 and Table 2). The Indigo Bunting, Blue Grosbeak, Yellow-breasted Chat and Yellowthroat all lie in the lower half of both graphs. James defines low to high values on her axis as going from open country to forest, low biomass to high biomass and xeric to mesic conditions, not unlike those described for my first discriminant axis. There is a difference in order of species between the two ordinations which can be partially explained by the presence of different species in the study areas. For example, the Indigo Bunting is a new species in southwestern Utah and several instances of interspecific competitive interactions have been reported for it with

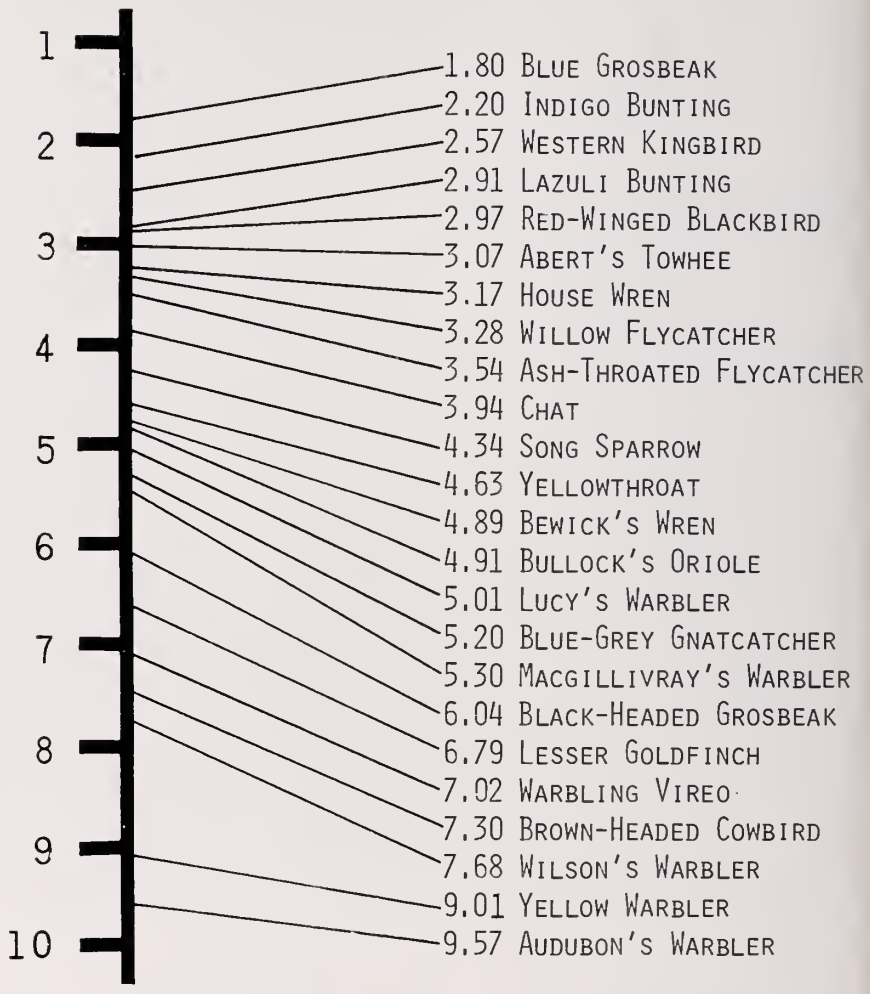

Fig. 1. Ordination of 24 Passerine species along the first discriminant function axis. Low values indicate areas of high ground cover and low canopy cover whereas high values indicate the more densely forested areas. 51.28% of the dispersion is accounted for by this axis.

its congener, the Lazuli Bunting (Whitmore, in press). This probably has an effect on the positioning of the two species along environmental gradients and could show up in a comparison of ordinations in areas of allopatry, such as Arkansas, and sympatry, such as Utah. Further research is currently being carried out in hopes of answering questions such as this.

As in my ordination, the Blue-Gray Gnatcatcher is found near the center

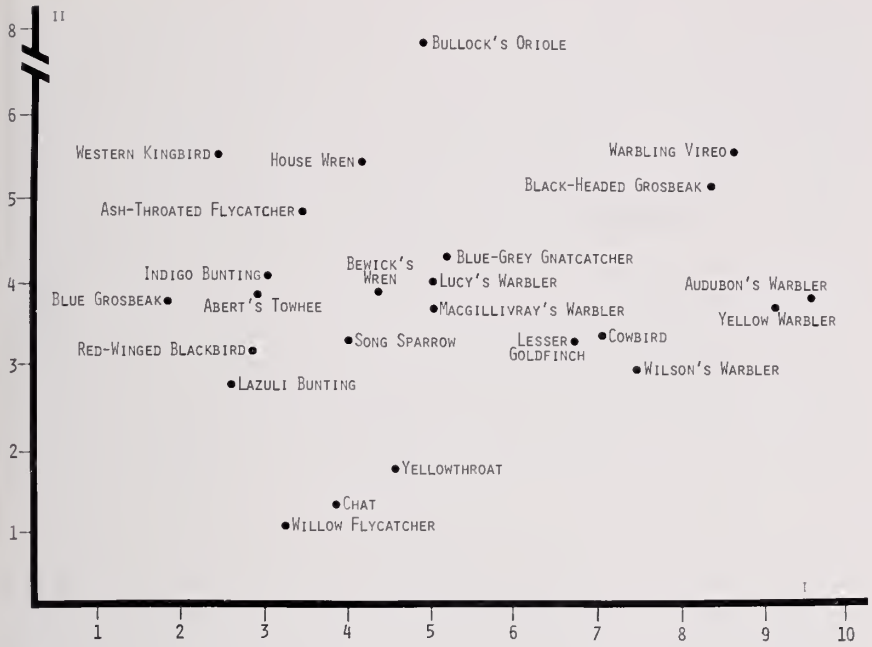

FIG. 2. A two-dimensional ordination using the first (I) and second (II) discriminant function axes. The first or horizontal axis is the same as in Figure 1. High values on the second axis correspond to the presence of large trees whereas low values indicate the absence of large trees. The second axis accounts an additional 18.10% of the dispersion for a total of 69.38% for the figure.

of the James ordination, a condition resulting from the species ability to show remarkable latitude in habitat use (often termed generalism in the literature). This is exemplified by looking at the various measurements obtained for individual birds of this species. For 21 individuals of the Blue-gray Gnatcatcher ground cover ranged from 15–80%, canopy height from 15–51 feet (4.6–15.5 m), canopy cover from 30–80% and shrub density from 10–70%. As a result its final position reflects an average of the extremes and places the bird near the middle of the graph.

In relation to other species present the Warbling Vireo is in an almost identical position on both graphs. In fact, James describes the same habitat as I found them to occur in, streamside cottonwoods (*Populus*) and willows (*Salix*).

I obtained a somewhat higher value for the Brown-headed Cowbird than did James, perhaps because of fewer tree-inhabitating granivorous birds in

my study area than hers, resulting in more latitude for the existing species in my area.

Note the position of the kingbirds in the two ordinations. The Eastern Kingbird is very rare in extreme southwestern Utah being replaced by the Western Kingbird. The Western Kingbird is not commonly found in Arkansas. The position of the two in the ordinations is almost identical indicating habitat or ecological replacement as well as geographic replacement. This phenomenon is also apparent in the now conspecific Bullock's and Baltimore orioles. A comparison of the original data in the two studies could be of interest for this species.

As defined by Goodall (1954) and further developed by Bray and Curtis (1957) an ordination is "an arrangement of units in a uni- or multi-dimensional order" as opposed to "a classification in which units are arranged in discrete classes." Whether the units are arranged using discriminant function analysis, principal components, similarity indices, a combination of these, or other techniques matters little if the results can be interpreted ecologically. Beals (1960) constructed an effective ordination using the Bray and Curtis (1957) coefficient of similarity while James (1971) used both principal components and discriminant function analysis. Both studies produced major contributions to the knowledge of avian ecology. Beals (1973) states that the coefficient of similarity ordinations produce results that are "ecologically more easily interpreted." However, ease of interpretation probably lies in familiarity with study sites and birds present, rather than the technique used.

As James (1971) mentions, care should be taken when analyzing the results obtained from ordinations using multivariate analysis since "the choice and number of variables may affect the results." This point is exemplified by examination of Figure 2. It would be a logical assumption that any species lying close to each other on the graph would occur together in nature. This assumption is true for the majority of cases. For example the Yellowthroat, Chat, and Willow Flycatcher are found together both on the graph and in nature. Another set of species commonly found in close association is the Lesser Goldfinch, Brown-Headed Cowbird, Wilson's Warbler, Yellow Warbler and Audubon's Warbler group. The Warbling Vireo and Black-Headed Grosbeak were almost always found together. Some abnormalities do occur in the ordination. Whereas the Indigo Bunting, Abert's Towhee, Bewick's Wren, Song Sparrow and Lazuli Bunting form an associated group in my study area, the Red-Winged Blackbird is seldom found with any of them even though they all have similar positions on the graph. This is brought about in part by the fact that even though the species had similar values of the most important variables, percent canopy cover, percent shrub density, number of trees 3–6 inches (7.6–15.2 cm) DBH and percent ground cover,

the method in which percent ground cover data were collected could not distinguish between bare ground and water. Consequently a marsh bird was placed with open shrub species. For ease in comparing my study and that of James the same variables were selected. In my study area other variables that could possibly be of importance include: litter depth, distance from water, the division of shrubs into size classes and others. Whether or not the addition of variables would provide a more effective ordination is unascertainable at this time.

The advantages of this type of analysis include the use of an easily programmable mathematical calculation, graphic results which are ecologically interpretable by a person with only limited knowledge of the technique, ease in comparison with other studies of a similar nature and lastly, according to Green (1971), the observed species diversity can often be explained by the distribution of species on variables which are a small subset of the possible ecological variables.

SUMMARY

A quantitative habitat ordination was carried out on 24 species of passerine birds inhabitating the riparian community of the Virgin River Valley, southwestern Utah. This work was compared to that of a previous study done by Frances James (1971). Many similarities were found between the two studies, including an interesting example of ecological replacements as exemplified by the Eastern and Western Kingbirds. Numerous differences were discussed and possible explanations for their appearance presented.

ACKNOWLEDGMENTS

I gratefully acknowledge the guidance and assistance from Dr. Clayton M. White during the course of this study. Dr. Frances C. James kindly read a draft of this work and her comments are greatly appreciated. Dr. Nathan Smith and Dr. Alvin Rencher aided with computer and statistical analysis. This work was supported in part by a D. Eldon Beck Scholarship from Brigham Young University, The Frank M. Chapman Fund of the American Museum of Natural History and the National Audubon Society.

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THE SYSTEMATIC POSITION OF THE GRAY CATBIRD (*DUMETELLA CAROLINENSIS*) AS INDICATED BY ITS NASAL MITES (ACARINA: DERMANYSSIDAE, RHINONYSSINAE)

Danny B. Pence and Stanley D. Casto

The Gray Catbird (*Dumetella carolinensis*) is presently considered to be a mimic thrush (Mimidae: mockingbirds and thrashers) (A.O.U. 1957). However, some of its characteristics suggest an affinity with true thrushes (Turdidae: thrushes, solitaires, and bluebirds). Coues (1927) noted the resemblance of Gray Catbird eggs to those of the Robin (*Turdus migratorius*). Similarities in nest construction by the Gray Catbird, Veery (*Hylocichla fuscesens*), and the Wood Thrush (*H. mustelina*) have also been described (Nickel 1965). The catbird's maxillo-palatines and other skeletal characters resemble those of the true thrushes and it has been stated that the catbird is nearer to the true thrushes than is any other mimid (Ridgway 1907:182). Indeed, a review of the synonymies reveals that the Gray Catbird has upon occasion been placed in the genus *Turdus* (Hellmayr 1934). Beecher (1953) found the jaw muscles, bill, palate, and tongue of the mimic and true thrushes to exhibit only minor variations. He dissected the catbird but apparently did not find evidence of a close relationship with the true thrushes. McCabe and Deutsch (1952) found the electrophoretic patterns of egg white proteins of the Gray Catbird, Brown Thrasher (*Toxostoma rufum*), Robin, and Eastern Bluebird (*Sialia sialis*) to be similar but drew no conclusion as to the relationship of the catbird and the true thrushes. Clark (1972) recently noted that mockingbirds and thrashers have a single large scute at the base of the two outer toes whereas *Dumetella* and the other genera of mimids have divided scutes. Divided scutes were also found in the Turdidae and several other families of passerines.

The foregoing observations suggest that the catbird may have affinities with both the Mimidae and Turdidae. To assess the parasite evidence relating to this question we surveyed the literature on rhinonyssine mites for records of infections from mimic thrushes, true thrushes, and related groups. Specimens of these mites were studied from Pence's collection. This evidence was evaluated with respect to the current hypotheses regarding the biology and systematics of the mites.

BIOLOGY OF THE MITES

The rhinonyssine mites are closely related to the dermanyssid nest parasites of birds (Domrow 1969). Rhinonyssines are obligatory parasites with the two genera most

commonly found in passerines occupying different niches within the nasal passageways. Species of the genus *Ptilonyssus* inhabit the turbinates whereas those of the genus *Sternostoma* are found in the deeper cavities of the infraorbital area. In their natural state rhinonyssine mites are sluggish and reddish-brown to transparent depending on their state of engorgement with blood. It has been hypothesized that rhinonyssines are transferred by direct contact with infected hosts either during courtship billing or by feeding of the young (Amerson 1969). Mites have been found in the nasal passageways of nestlings (Porter and Strandtmann 1952, Terbush 1963, Amerson 1969) suggesting that the latter method is important. If indeed the transfer of mites depends on the reproductive activities of the host there should be virtually no interspecific transmission of mites. Reproductive isolation of the avian hosts should ensure that their mites are also reproductively isolated from those mites occurring in closely related species of birds. Since parasites presumably evolve at a somewhat slower rate than their hosts, the similarity of mites from different host species should serve as an index of the relationship of the hosts.

Although the systematics of rhinonyssine mites are somewhat confused, the species discussed herein are easily differentiated on the basis of the number and shape of the dorsal plates and chaetotaxy (number, arrangement and shape of setae) of the idiosoma (body) and legs. The genus *Sternostoma* is divided into two major groups depending on the presence of either one (Figs. 1–3) or two (Figs. 4, 5) dorsal plates. *Ptilonyssus euroturdi* from the Gray Catbird (Fig. 8) is separated from the two closely related species of *Ptilonyssus*, *P. mimi* and *P. toxostomae* (Figs. 6–7), occurring in other mimic thrushes by the shape of the dorsal plate and chaetotaxy of legs I and IV.

RESULTS AND DISCUSSION

The species of rhinonyssine mites infecting birds of the families Mimidae, Turdidae, and Cinclidae (Dippers) are listed in Table 1. The Gray Catbird is infected with mite species found in both the Turdidae and the Mimidae. The Gray Catbird harbors *Sternostoma dumetellae* (Pence 1972a), a species which has not been recorded from any other mimid. This mite is a member of a small complex of closely related species that includes *S. technaui* and *S. spathulatum*. These two species are recorded primarily from turdids. *Sternostoma dumetellae* is differentiated from *S. technaui* and *S. spathulatum* on the basis of differences in chaetotaxy (Pence 1972a) (Figs. 1–3).

Sternostoma kelloggi is reported from the Gray Catbird (Hyland and

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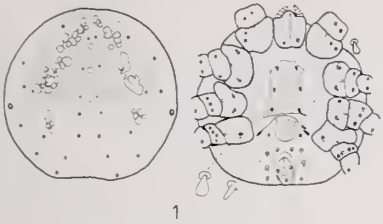
Figs. 1–8. Rhinonyssine nasal mites from North American mimic and true thrushes. 1. Dorsal and ventral view of idiosoma, respectively, of *Sternostoma dumetella* from Catbird. 2. Same as above, *S. technaui* from American Robin. 3. Same as above, *S. spathulatum* from Hermit Thrush. 4. Dorsal and ventral views of idiosoma, respectively, and ventral view of tarsus IV of *S. hutsoni* from Swainson Thrush. 5. Same as above, *S. kelloggi* from Brown Thrasher. 6. Dorsal view of leg I, ventral view of leg IV, and dorsal and ventral views, respectively, of idiosoma of *Ptilonyssus toxostomae* from Brown Thrasher. 7. Same as above, *Ptilonyssus mimi* from Mockingbird. 8. Same as above, *Ptilonyssus euroturdi* from Catbird.



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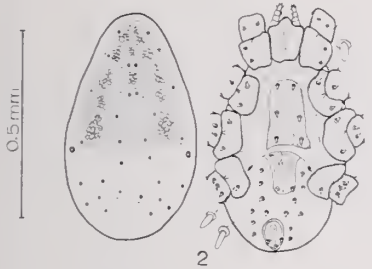

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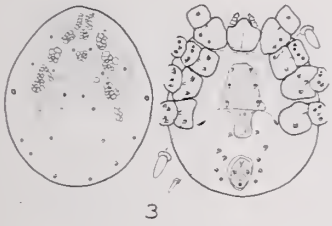

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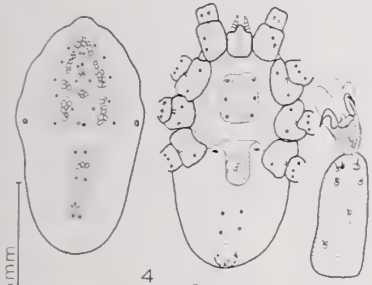

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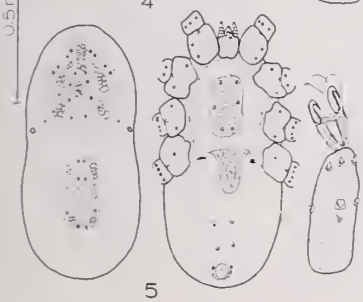

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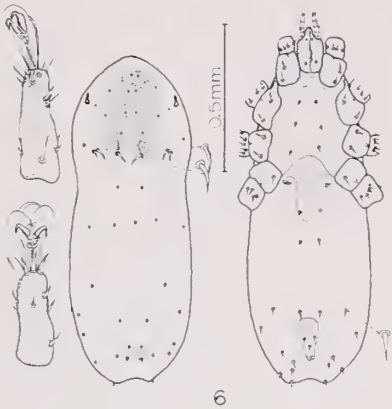

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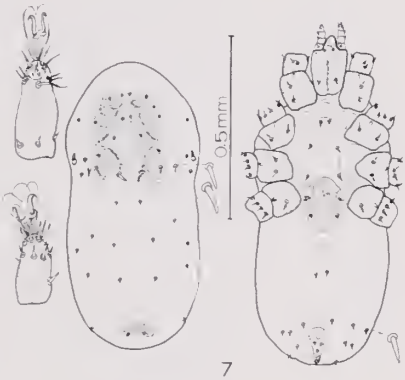

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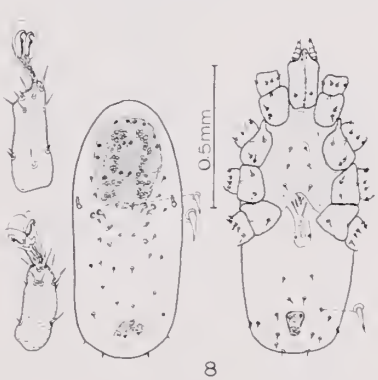

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Table 1

Rhinonyssine Mites Infecting Birds of the Families Mimidae, Turdidae, and Cinclidae

Mite Species	Host Species	Locality	Authority
	Turdidae		
Sternostoma dureni	*Oreocinclata lunulata*	Australia	Domrow 1969
	Turdus olivaceus	Africa	Fain 1957
S. hutsoni	*Hylocichla ustulata*	California	Furman 1957
	Turdus nudigenis	Trinidad	Fain and Aitken 1967
S. sialiphilus	*Sialia sialis*	Michigan	Hyland and Ford 1961
		Louisiana	Pence 1972a
S. spathulatum	*Hylocichla fuscescens*	Cuba	Černý and Dusbàbek 1970
	H. guttata	Louisiana	Pence 1972a
	H. ustulata	California	Furman 1957
S. technaui	*Mimocichla plumbea*	Cuba	Dusbàbek 1969; Černý and Dusbàbek 1970
	Oreocinclata lunulata	Australia	Domrow 1969
	Turdus ericetorum	Belgium	Fain 1963
	T. fumigatus	Trinidad	Fain and Aitken 1967
	T. migratorius	Louisiana	Pence 1972a
	T. musicus	Belgium	Fain 1963
	T. nudigenis	Trinidad	Fain and Aitken 1967
	T. olivaceous	Africa	Zumpt and Till 1955
	T. pilaris	Belgium	Fain 1963
Ptilonyssus eurotardi	*Hylocichla mustelina*	Louisiana	Pence 1972b
	Mimocichla plumbea	Cuba	Černý and Dusbàbek 1970
	T. ericetorum	Belgium	Fain and Hyland 1963
	T. fumigatus	Trinidad	Fain and Aitken 1967
	T. merula	New Zealand	Domrow 1972
	T. nudigenis	Trinidad	Fain and Aitken 1967
	T. philomela	New Zealand	Domrow 1972
	T. viscivorus	Belgium	Fain and Hyland 1963
P. afroturdi	*T. olivaceus*	Africa	Fain 1962
P. sialiae	*Sialia currucoides*	Texas	George 1961
	Mimidae		
S. dumetellae	*Dumetella carolinensis*	Louisiana	Pence 1972a
S. kelloggi	*D. carolinensis*	Michigan	Hyland and Clark 1959
	Mimus polyglottos	Cuba	Černý and Dusbàbek 1970
	Toxostoma rufum	Louisiana	Pence 1972a
P. eurotardi	*Dumetella carolinensis*	Michigan	Fain and Hyland 1963
		Louisiana	Pence 1972b
P. mimi	*Mimus polyglottos*	Texas	George 1961
		Louisiana	Pence 1972b
P. toxostomae	*Toxostoma rufum*	Louisiana	Pence 1972b

TABLE 1 (continued)

Mite Species	Host Species	Locality	Authority
	Cinclidae		
S. technaui	*Cinclus cinclus*	Europe	Vitzthum 1935, Fain 1963
	C. pallasi	Russia	Bregetova 1965

Clark 1959), Brown Thrasher (Pence 1972a), and Mockingbird (Černý and Dusbábek 1970). Although *Sternostoma kelloggi* is a distinct species, it is closely related to *S. hutsoni*, *S. sialiphilus*, and *S. dureni* from New and Old World turdids (Furman 1957, Fain 1957, Fain and Aitken 1967, Hyland and Ford 1961) (Figs. 4–5).

Records of the genus *Ptilonyssus* further substantiate the relationship of the Gray Catbird with the Turdidae. The single species recorded from the Gray Catbird is *P. euroturdi*. This species has also been recorded from a variety of turdids in both the New and Old World (Fain and Hyland 1963, Fain and Aitken 1967, Pence 1972b, Domrow 1972) (Fig. 8). A similar species, *P. afroturdi*, has been reported from an African turdid (Fain 1962). The species of *Ptilonyssus* from the Mimidae are represented by two very closely related forms, *P. mimi* and *P. toxostomae*. These two species are quite distinct from *P. euroturdi* with major differences in both the chaetotaxy and shape of the dorsal plates (Figs. 6–8). These species are reported from the Mockingbird and Brown Thrasher in North America, respectively (George 1961, Pence 1972b). An additional species, *Ptilonyssus sialiae*, described from the Mountain Bluebird (*Sialia currucoides*) (George 1961) is not morphologically related to the above forms. Thus, on the basis of evidence from its rhinonyssine mites the Gray Catbird appears to have affinities with both the Mimidae and Turdidae. The morphological relationships of these mites are illustrated in Figs. 1–8.

Ridgway (1907) believed that the Turdidae, Mimidae, and Cinclidae were related families. Beecher (1953) recognized the Turdinae, Miminae, and Cinclinae as subfamilies of the Turdidae. The parasite evidence supports systematic association of these three groups. *Sternostoma technaui* is recorded not only from mimids and turdids, but also from *Cinclus cinclus* in Europe (Vitzthum 1935) and *Cinclus pallasi* in Russia (Bregetova 1965).

The alleged relationship of the Mimidae and the Troglodytidae (Wrens) (Coues 1927, Hohn 1973) is not supported by this parasite evidence. Three species of *Ptilonyssus* have been reported from wrens. *Ptilonyssus salpinctis* is described from the Rock Wren (George 1961), *P. troglodytis* from the

Winter Wren (Fain 1964), and *P. thyrothori* from the Carolina Wren (Pence 1972b). These species do not appear to be closely related to those species of *Ptilonyssus* reported from the mimids.

A major problem in determining avian affinities from parasite evidence is the lack of precise information on host specificity and other host-parasite relationships. Inferences must necessarily be drawn from incomplete collection records and inadequate knowledge of the biology and systematics of both the host and its parasites. The criticism of Stresemann (1959) concerning the exaggerated use of parasite evidence is justified. This host-parasite information should be considered in proper perspective and in concurrence with that derived from all other contributing disciplines. The parasite evidence for the relationships of the birds discussed herein assumes an acarine infection of the ancestral hosts and the evolution of a mode of transfer that precludes interspecific transmission between hosts. Should additional studies demonstrate the validity of the assumptions, the rhinonyssine mites may well become an additional tool for use in avian systematics.

SUMMARY

The rhinonyssine nasal mite literature was surveyed for records of infection of the Mimidae, Turdidae, and related groups and these data were evaluated with respect to the systematic position of the Gray Catbird (*Dumetella carolinensis*). The Gray Catbird harbors *Sternostoma dumetellae*, a species not recorded from other mimids but closely related to *S. technaui* and *S. spathulatum* which are recorded from the Turdidae and Cinclidae. *Sternostoma kelloggi* from the Gray Catbird, Brown Thrasher, and Mockingbird is a distinct species but again closely related to *S. hutsoni*, *S. siaphilus*, and *S. dureni* from the New and Old World Turdidae. *Ptilonyssus euroturdi* from the Gray Catbird is also found in a number of turdids in both the New and Old World. Thus, the parasite evidence suggests that the Gray Catbird has affinities with both the Mimidae and Turdidae. The occurrence of *Sternostoma technaui* in the Mimidae, Turdidae, and Cinclidae also suggests relationship among these families.

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Dept. of Veterinary and Zoological Medicine, Texas Tech Univ. School of Medicine, Lubbock, TX 79409. Accepted 13 Sept. 1974.

NEW LIFE MEMBER

A new addition to the list of life members of the Wilson Ornithological Society is Dr. Pershing B. Hofslund. Dr. Hofslund has held four offices in the Wilson Society and was President of our Society from 1971–1973. He has been editor of The Flicker, president of the Minnesota Ornithological Union, and is an elective member of the AOU. Dr. Hofslund's principal interests in ornithology include hawk migration and wood warbler life histories; he has published approximately 75 of his studies. Presently Professor of Biology at the University of Minnesota, Dr. Hofslund is also active with the Arrowhead Zoological Society and is on the State Board of the Minnesota Zoological Gardens. Dr. Hofslund is married and has two children.

HABITAT SELECTION BY WATERFOWL OF ARGENTINE ISLA GRANDE

Milton W. Weller

Isla Grande is the main island of the archipelago at the tip of South America known as Tierra del Fuego. Current knowledge of the birds of Isla Grande has been ably summarized by Humphrey et al. (1970). As part of a study of austral waterfowl, I spent the period from 10 January to 9 February 1972 at three locations on Isla Grande. I recorded 84 of 108 bird species recorded by Humphrey et al. (op. cit.), including 15 of the 17 known species of waterfowl. The purpose of this paper is to discuss habitat selection of Isla Grande waterfowl. Observations are also presented on their parental care, brood sizes and reproductive behavior. Data on stage of the reproductive cycle were gathered by age classification of broods according to the system described by Taber (1969:330): Class I = downy young; II = partly down and partly contour feathers; III = full juvenal body plumage but not yet flying.

Observations spanned two major study areas, the southern mountainous beech forest along the Beagle Channel and the open steppe zone of northern Isla Grande. Nineteen days were spent at Estancia Harberton on the Beagle Channel, four days from Ushuaia west to Lapataia, and nine days at Estancia Viamonte and the region west and north of Rio Grande (Fig. 1).

STUDY AREAS

Estancia Harberton is along the Beagle Channel in an area of shoreline highly dissected with estuaries, bays and offshore islands. The terrain is rolling at sea level, rising in a series of hills to mountains of nearly 915 m. Treeline is reached at about 518 m. The vegetation near the sea is meadow of bluegrass (*Poa* spp.) and tall rush (*Marsippospermum grandiflorum*) a few meters wide, changing to heath of fachine (*Chiliotrichum diffusum*), barberries (*Berberis ilicifolia*, *B. empetrifolia*, and *B. buxifolia*), and diddle-dee (*Empetrum rubrum*). In protected areas or high elevations, three species of beech (*Notofagus* spp.) surround bays, lakes, streams and bogs; in very wet places only the smallest southern beech species, *N. antarctica*, is common.

The flooded upper reaches of estuaries (creeks) are silt-covered gravel or pure silt. Extensive salt meadow may be adjacent. Seashores are gravel, with occasional large boulders but no exposures of extensive rock outcrops at low tide. There are no true barrier ponds along the coastline, but alluvial materials deposited at the mouths of larger streams slow the current and produce lake-like conditions or wet meadows attractive to waterbirds.

Lakes that I encountered were shallow, with gravel or rock bottoms and edges, the water was stained with tanin, acid (pH 4.8–5.0 for three tested) and cold. Rivers meander in broad valleys near the sea, but cut more restricted channels in the extensive gravel beds. There is one series of waterfalls on the Rio Lashifashaj that produces

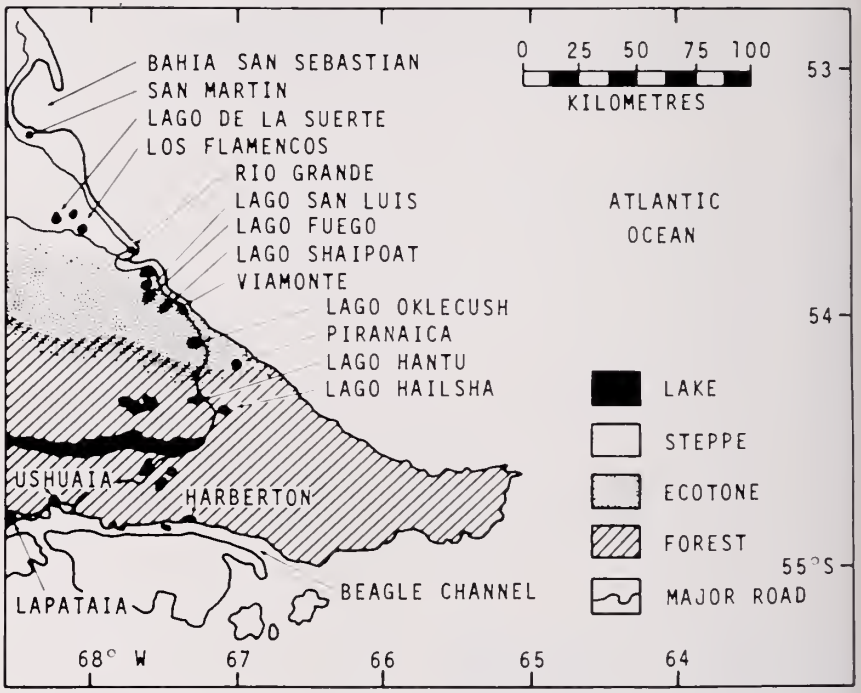

FIG. 1. Map of place names mentioned in the text on Argentine Isla Grande. After Humphrey et al. (1970) and Goodall (1970).

cascading water over a stretch of 100 m; otherwise, torrents were not encountered at low altitudes near the coastline. Smaller streams meander through rather dense forest and often are overgrown by trees, as such sheltered valleys induce tree growth by affording protection from the wind. Oxbow lakes are rare, but were present on the Rio Cambaceres; some meadow-bog areas obviously are overgrown oxbows.

The introduction of beavers into Tierra del Fuego in the 1940s, and their spread to the Harberton area in the 1950s, has resulted in dams along numerous small streams. The ponds so formed are extensive, linear patches of flooded and dead timber, which often are rich in invertebrates and attractive to birds. Unflooded bog meadows rarely have sufficient standing water to be attractive to ducks but they are used by grazing Upland Sheldgeese (*Chloephaga picta*).

The habitat from Ushuaia to Lapataia is similar in character to that at Harberton, but the Beagle Channel is broader, the coastline less sheltered, and the lakes are larger.

Estancia Viamonte, located along the east coast at 54°40′S, is in the transition zone between southern forest and northern steppe. The land is rolling grassland with some sizable patches of southern beech, often of dwarfed growth form on hilltops. Lakes and marshes are found in depressions in the morainal hills. Approximately 10 km north of Viamonte is the last grove of forest along the coast; the northern part of Isla Grande is treeless grassland extending to the Straits of Magellan and west to the border of Chile.

ANNOTATED LIST

Coscoroba Swan (*Coscoroba coscoroba*).—This bird was seen only on Lago Rio Fuego, a large and sparsely vegetated marsh about 10 km WNW of Estancia Viamonte. Five seemingly flightless birds were sitting in open water and two fully-winged birds were sitting on shore.

Black-necked Swan (*Cygnus melanocoryphus*).—This species was seen regularly at large marshes or marshy lake edges in open country from Lago Fagnano northward. The largest number was 81 at Lago Hantu, 15 km north of Lago Fagnano. A total of four broods was seen at Lago Shaipoat, Lago Rio Fuego, and Lago Oklecush, and ranged from 1 to 4 young (mean = 2.8).

Ashy-headed Sheldgoose (*Chloephaga poliocephala*).—Although considered a bird of forested regions (Humphrey et al. 1970), flocks of these geese were common both in forest clearings along the Beagle Channel and at barrier ponds and grassy ecotones near Viamonte. The species was not seen in the open steppe north of Viamonte although nonbreeding birds probably occur there. A pair and five Class II young were seen in meadow-like islands where the Rio Cambaceres winds through dense forest east of Harberton.

Ruddy-headed Sheldgoose (*Chloephaga rubidiceps*).—The disappearance of this species from the entire steppe area where it once was considered the most abundant (Scott 1954) or second most abundant sheldgoose (Ripley 1950) is cause for great concern. No broods or young were seen, and only five pairs and a single were observed. These were in dry grassland near the Rio San Martin on San Sebastian Bay. This decline may be a product of intensive control and bounties paid by the government and rural societies which, in the summer of 1972–73, spent about $7500 U.S. for 150,000 eggs collected and destroyed (Mrs. Tom Goodall, pers. comm.). Although most eggs probably were those of the more abundant Upland Sheldgoose, eggs of the Ruddy-headed Sheldgoose also would have been destroyed. Another possible influence may be intentional introduction of the Patagonian race of the fox, *Dusicyon griseus* which now is very common in the steppe country. Currently, this sheldgoose is doing well only on the Falkland Islands (Weller 1972), but control programs there could threaten the survival of the entire species.

Upland Sheldgoose (*Chloephaga picta*).—This species was ubiquitous and abundant. A total of 122 broods of all ages was seen in all areas during January and early February, with Class II predominating. Broods ranged up to 13 young with a mean of 4.4. Both parents were associated with the brood in 82% of my observations. Some males wait or feed some distance from the brood on a prominent site from which they alert the female by their quiet whistling call. Such males usually fly to the female and young as they move to open water where the brood waits until the potential danger has passed. Depending on the number of broods involved and the observer's approach, males sometimes are difficult to associate with specific broods. This may also account for unusual cases where two males accompany one female and brood. Occasionally, two hens with broods join, and this may be responsible for the broods with up to 22 young of mixed ages, but having only one female. Such pooling also may explain the unusual pattern of increasing rather than decreasing brood size with advancing age class (Table 1).

One nest of an Upland Goose was discovered on 14 January on a hill overlooking a large bay. The nest was under a barberry bush, known locally as calafate (*Berberis buxifolia*), in open forest. The male waited about 10 m away where a mound of droppings indicated a loafing site providing clear visibility of a wide area.

Table 1

Mean Sizes of Broods of Upland Sheldgeese Arranged by Age Classes, Argentine Isla Grande, 10 January to 9 February 1972

Age Class		Beagle Channel	Forest-Steppe Ecotone	Total
I	Mean (N)	3.65 (40)	4.55 (11)	3.84 (51)
	S.D.	1.94	1.97	1.96
II	Mean (N)	4.70 (87)	4.28 (18)	4.63 (105)
	S.D.	2.29	2.08	2.25
III	Mean (N)	5.57 (7)	5.25 (4)	5.45 (11)
	S.D.	3.91	0.96	3.08
TOTAL	Mean (N)	4.43 (134)	4.48 (33)	4.44 (167)
	S.D.	2.34	1.92	2.26

Kelp Sheldgoose (*Chloephaga hybrida*).—Contrary to the general statement in Humphrey et al. (1970), I did not find this species abundant on the Beagle Channel during the breeding season. My only records were two pairs and a male seen loafing on the barrier sand at the mouth of the Rio Lashifashaj, west of Harberton, and a pair seen east of Harberton feeding in the very narrow *Porphyra* zone along the Beagle Channel. I suspect that breeding pairs are on still more exposed coastlines where suitable marine algae grow on rock outcrops. The species becomes common in Ushuaia in fall and winter (Mrs. Tom Goodall, pers. comm.). On the Viamonte coastline, flocks of up to 150 were present on the extensive tidal flats in early February, when other sheldgeese were still rearing young.

Crested Duck (*Lophonetta specularioides*).—Humphrey et al. (1970) found little evidence of breeding, but I noted numerous broods at Harberton in estuaries and quiet bays, and others were seen at Lago Fuego and Lago Shaipoat, west of Viamonte. The 11 broods seen ranged from 1 to 7 young (mean = 3.4) mostly of Class I and II, suggesting that most had hatched in early to mid-January. Concurrently, large flocks of adults were present both in Harberton and along the northeastern coast, suggesting that birds here, as on the Falkland Islands, may not breed at one year of age. Although Crested Ducks were found mainly along the coast of the Beagle Channel, they also were common in brackish, inland lakes such as Laguna de la Suerte, 8 km west of Estancia Los Flamencos.

Flightless Steamer-Duck (*Tachyeres pteneres*).—This species was abundant and well-spaced along virtually all coastline and bays in the Harberton area, but was not seen on the northeastern coast. Nine pairs had broods in January (range = 1 to 6 young; mean = 3.4), and territorial behavior was common. One nest hatched on 12 January on the Harberton peninsula. The broods were seen in all types of coastal areas except estuaries. About 100 flightless birds, probably nonbreeders, were seen along the Beagle Channel on 14 January.

This species is not known at Viamonte (Humphrey et al. 1970) due perhaps to the extreme tides and to the rock shelves bordered by abrupt cliffs that extend seaward for kilometers at low tide. Not only would the extensive shelves strand flightless birds at low tide, but the cliffs might prevent movement of females into the uplands for nesting.

Flying Steamer-Duck (*Tachyeres patachonicus*).—This species occurred on both southern and northeastern coasts, but was the only steamer-duck found on the northeastern coasts. Along the southern coast, it occurred only in estuaries, quiet channels or in large freshwater lakes. There, all six broods seen were in or near estuaries, whereas pairs without broods frequented other habitats. Little interspecific aggressiveness was noted, and breeding pairs seemed to be isolated in part by habitat preference. Habitat conditions on the eastern coast are not conducive to brood rearing, and the four broods seen were in large lakes in the steppe zone. The 10 broods observed in both areas had from 1 to 6 young (mean = 3.4).

Spectacled Duck (*Anas specularis*).—Although this bird often is associated with large, slow-moving streams and their valleys (Humphrey et al. 1970, Weller 1968), the only birds seen were in natural or beaver-formed lakes in the forested mountain area near Lapataia and Harberton. Two were seen loafing on an island shore at the outlet of Lago Roco, where the species also had been seen by Keith (1970). A pair was observed on an unnamed lake north of Harberton, and two were seen on the Beaver Lakes east of the Rio Cambaceres at Harberton. The female of one pair gave the dog-like *arf-arf* call, and the male weakly whistled *wee, wee, wee*. T. L. Bridges states (pers. comm.) that they are very rare in the ecotonal area near Viamonte.

Speckled Teal (*Anas flavirostris*).—This adaptable teal was present in flocks of up to 175 in the northern freshwater marshes and lakes, where a few flightless adults were observed. Most Speckled Teal in the coastal zone were found as small flocks of 4 to 24 birds feeding at low tide on the mud flats of upper estuaries. This teal, known locally as "mud" teal, characteristically feeds at the edges of lakes or marshes and on the mud flats of streams and estuaries. Five broods (range = 3 to 5; mean = 3.4) were seen, three in the steppe marshes and two in forested beaver ponds near Harberton.

Southern Wigeon (*Anas sibilatrix*).—This herbivorous duck was seen in both habitat regions, but was uncommon to rare in the forest zone. It occurred along slow-moving rivers, where one brood was seen, or on lakes with adjacent meadows. The species was seen on many lakes in the ecotonal area. About 5000 molting birds were seen on Lago Hantu. Three pairs with broods were seen at Lago Oklecush and one brood was seen in the meadows along the Rio Varela. The four broods ranged from 2 to 7 young and averaged 4.0.

Yellow-billed Pintail (*Anas georgica spinicauda*).—The distributional pattern of this species was comparable to that of Speckled Teal except that flock size averaged larger and that birds used more diverse types of steppe lakes. Like that species, this pintail occurred in estuaries in the Harberton area, but it dabbles and upends in deeper water than do teal. One brood of four young and four flightless adults also were seen at Lago Oklecush. Yellow-billed Pintails seem to be an early nesting species, and I suspected that many of the birds seen were flying young-of-the-year.

Silver Teal (*Anas versicolor*).—I noted this species on only one occasion near Viamonte, when two or three were seen at Lake Shaipoat. Residents consider the bird uncommon to rare, and breeding records are lacking. It has not been reported in the forest zone.

Red Shoveler (*Anas platalea*).—The shoveler did not occur in the forest lakes along the Beagle Channel, but flocks of 40 to 80 were seen at rather open lakes, such as Lago Shaipoat and the San Luis lakes near Viamonte. These birds were filter feeding.

Torrent Duck (*Merganetta armata*).—Humphrey et al. (1970) noted that this species had been extirpated in some areas and no extant populations were known to them on Isla Grande. Although I did not see the birds, I saw suitable habitat north of Harberton on the cascades of the Rio Lashifashaj. Mr. and Mrs. Tom Goodall have seen Torrent

Ducks there many times, including as late as January 1972 (R. N. P. Goodall and J. Boswell, ms.).

BROOD REARING

Mid-January to mid-February obviously is the brood rearing period among waterfowl of Tierra del Fuego. I found only two active nests (Upland Goose and Flightless Steamer-Duck) and most young already were several weeks old and in Age Class II. Four Yellow-billed Pintails, at least three Speckled Teal, 100 or more Flightless Steamer-Ducks, and thousands of Southern Wigeon were flightless in the post-nuptial molt. Based on this sampling period, there was little evident range in chronology of nesting although the sheldgeese, Yellow-billed Pintail, Speckled Teal, and Southern Wigeon probably nested earliest.

Males of southern hemisphere anatids tend to remain with and assist in protecting the brood whereas northern hemisphere ducks rarely do so. A total of 218 broods of nine species of waterfowl were seen. The pair was in attendance in all broods observed of five species: Ashy-headed Sheldgoose (one brood observed), Yellow-billed Pintail (one brood), Black-necked Swan (four broods), Flightless Steamer-Duck (nine broods), and Southern Wigeon (four broods). In other species, attendance by both members of the pair ranged from 60 to 91%: Speckled Teal (60.0), Flying Steamer-Duck (80.0), Upland Sheldgoose (82.0), and Crested Duck (90.9). The remaining broods had only the female attendance except for 2.4% of Upland Sheldgoose broods in which males alone were in attendance. One brood of Upland Sheldgoose seemed unattended.

DISCUSSION

Recent studies of many groups of birds demonstrate that habitat selection forms one of the major means of avoiding competition among closely related species (MacArthur 1958, Lack 1971). Little work has been done on waterfowl, though Lack (1971) has pointed out general differences in habitat and feeding behavior which may isolate different species. Frith (1959) noted the manner in which Australian ducks not only specialize on different foods but breed at different times of year in relation to water availability.

Most species of waterfowl on Isla Grande breed concurrently during the warm summer season but seem to be habitat-segregated, and probably differ in food use. This pattern is comparable to that observed on the Falkland Islands (Weller 1972), but I was unable to collect birds to support observations on feeding habits of waterfowl on Isla Grande. The distribution of the sheldgeese is a good example of presumed ecological isolation during the breeding period. Kelp Sheldgeese occur only along exposed, rocky seashore.

Upland Sheldgeese occur on shortgrass meadows in open or semiwooded country. Ashy-headed Sheldgeese nest in more densely forested areas along streams or lakes, but post-breeding flocks or nonbreeders use open meadows and at times associate with Upland Sheldgeese. Ruddy-headed Sheldgeese are found only in the drier steppe areas of northern Isla Grande, but how they are isolated from Upland Sheldgeese is not clear. On the Falkland Islands, Ruddy-headed Sheldgeese are most prevalent on the drier, western islands than in the eastern, wetter areas (Weller 1972), and probably occur in the taller grasses.

Greatest overlap in habitat use occurs among ducks that use concentrated food resources, as seems true in freshwaters of the Falkland Islands (Weller 1972) and in estuaries in England (Olney 1963). Even in food-rich habitats, the species tend to have different feeding adaptations and behavior so that direct competition may be reduced. The Speckled Teal feeds in very shallow and often muddy areas where its short neck is efficient and the finely lamellated bill strains minute organisms (Weller 1972). Yellow-billed Pintail feed in deeper water and they can reach benthic organisms that few other ducks could obtain. Red Shovelers are more often in open and unvegetated marshes or lakes, presumably where crustaceans are abundant. In deeper lakes, Flying Steamer-Ducks feed on the bottoms by diving. Southern Wigeon seem to be strictly herbivorous and frequent dense beds of submergents in open water.

In estuaries, Speckled Teal and Brown Pintails in the post-breeding season often segregate in much the same manner as do breeding birds or flocks in freshwater. Crested Ducks, which are more common in estuaries than lakes, favored gravel-silt areas of more saline sites and thus do not feed in areas used by pintails or teal. Because they feed by diving, steamer-ducks probably overlap little in food use with dabbling ducks. The preference of Flying Steamer-Ducks for estuaries may not reflect a preference for saline areas but for quiet waters because nonbreeding pairs of this species were seen only in protected marine bays and channels. Magellanic Flightless Steamer-Ducks, with or without broods, were the species seen in open and often rough water along unprotected shorelines.

Two species of ducks reported as formerly breeding (Torrent Duck by Humphrey et al. 1970) or possibly breeding (Rosy-billed Pochard, *Netta peposaca*, by Olrog 1968) were not seen. Obviously, habitat and foods of the Torrent Duck would not overlap with any of the above species. Rosy-billed Pochards feed in a manner similar to Flying Steamer-Ducks but are restricted to freshwaters where some competition could occur. However, this pochard is dominantly a bird of pampas marshes and is rare in Tierra del Fuego. Although these observations need to be supported by detailed studies

of food habits, observations during the brood rearing period infer that most species are isolated by habitat selection and feeding behavior.

SUMMARY

During a month-long study of habitat selection and feeding behavior of waterfowl on Argentine Isla Grande, 15 of the 17 species of waterfowl were seen. Habitat segregation of breeding waterfowl was quite distinctive and resembled the pattern of the same species in the Falkland Islands. Dabbling ducks of the genus *Anas* overlapped most in freshwater marshes but, even there, seemed to be segregated by feeding sites and feeding behavior.

ACKNOWLEDGMENTS

Field work was sponsored by NSF Grant GV-21491 to Iowa State University. I am particularly indebted to Natalie and Tom Goodall of Estancia Harberton, who provided facilities, technical assistance and information on local flora and fauna that made the study possible. Adrian and Stefanie Goodall, and others of Estancia Viamonte, graciously offered housing and transportation, and Thomas Leonard Bridges provided a great deal of insight into the natural history of the area. Helpful comments on an earlier draft of the manuscript were received from Mrs. Tom Goodall and Dr. Philip Humphrey. This is Journal Paper No. J-7819 of the Iowa Agriculture and Home Economics Experiment Station, Ames, Iowa. Project 1969.

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DEPT. OF ZOOLOGY AND ENTOMOLOGY, IOWA STATE UNIV., AMES, IA 50010 (PRESENT ADDRESS: DEPT. OF ENTOMOLOGY, FISHERIES & WILDLIFE, UNIV. OF MINNESOTA, ST. PAUL, MN 55108). ACCEPTED 27 JULY 1974.

SOLAR RADIATION, LIGHT INTENSITY, AND ROOSTING BEHAVIOR IN BIRDS

Palmer E. Krantz and Sidney A. Gauthreaux, jr.

Many investigators have commented on the apparent relationship of cloud cover, light intensity, temperature and sunset time to the time of roosting in many bird species (e.g., Davis 1955, Bliese 1955, Davis and Lussenhop 1970). There is general agreement that light levels are closely associated with the timing of roosting responses, but there is disagreement concerning the influence of cloud cover, temperature, and time of sunset on the daily onset and termination of roosting. We have obtained data that clarify the issue. Furthermore, we report a close relationship between the amount of daily solar radiation and the arrival time of birds at the roost. This latter relationship is important as a field verification of the circadian rule (Aschoff 1967).

MATERIALS AND METHODS

Observations were made on 21 afternoons during February and March, 1972, at a Brown-headed Cowbird (*Molothrus ater*) roost located in a bamboo (*Phyllosatachys* spp.) thicket on the campus of Clemson University, South Carolina. The roost contained on an average 1500 birds, and only "pre-roosting" and "roosting" behaviors were studied (Jumber 1956). The roost site consisted of a bamboo area of approximately 19 m^2 surrounded by four isolated trees; the bamboo was about 4 m high, and the nearby trees ranged from 10 to 16 m in height. All data were gathered 20 m from the roost. The following information was taken each day: general weather conditions; direction of flight into the roosting area; time of first flock arrival, peak of pre-roosting activity, first bird into the roost, peak of roosting activity and last bird into the roost. The light levels near the termination of roosting behavior were based on the light level required to activate a photocell-controlled light 2 m from the roost. We found that the light consistently turned on at an ambient light intensity of 64.56 lux (6 ft-candles). A Weston photometer (Model 703-67) was used for light measurements. Data on total daily solar radiation and average daily temperature were supplied by the National Weather Service office on campus.

RESULTS

Most of the flocks that arrived at the roost site contained from 10 to 30 birds, but occasionally flocks had 200 to 250 birds. The birds landed in the trees next to the roost (pre-roosting behavior) and did not fly into the bamboo thicket until nearly all the flocks had assembled in the nearby trees. On the average approximately 28 min elapsed between the arrival of the first and last flocks in the trees. Coincident with the arrival of the last flock, the birds that had assembled in the pre-roosting trees started to enter the roost. Figure 1 shows the plots of the time the first birds entered the roost, the time the

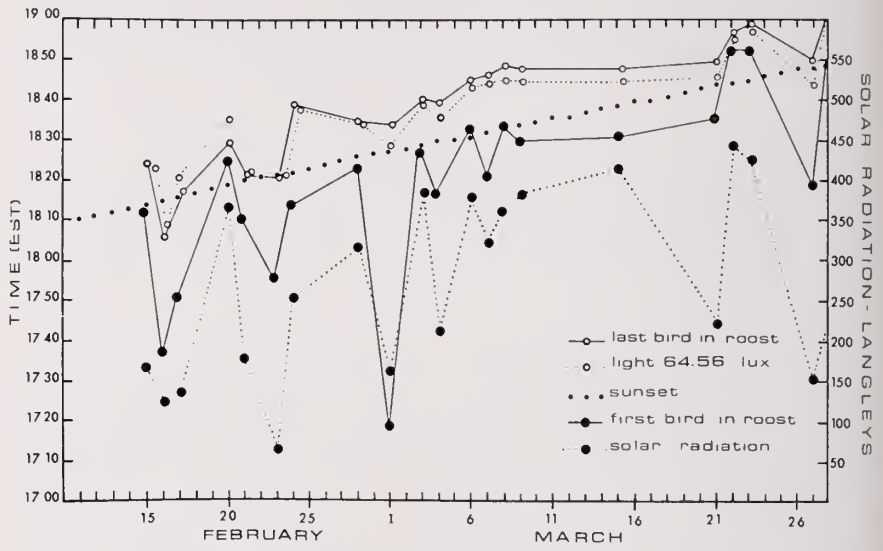

FIG. 1. Plots of first and last birds in roost in relation to daily amount of solar radiation, time of sunset, and time that light levels reached 64.56 lux. Twenty-one days were sampled from February 15 to March 28.

last bird entered the roost, the total daily solar radiation, and the time when ambient light intensity reached 64.56 lux. The curves for the first bird in roost (the same as peak number of birds in nearby trees) and the total daily solar radiation show very close correlation. The product moment correlation coefficient (Sokal and Rohlf 1969) for these two curves is +0.67 ($P < .001$). We found the degree of association between the time of onset of pre-roosting behavior and the amount of daily solar radiation to be equally strong. Similarly, the plots of the time when the last bird entered the roost and the time when ambient light levels reached 64.56 lux show a marked degree of association. The product moment correlation coefficient for these plots is +0.99 ($P < .001$).

Despite fluctuations in the curve for the times that the first birds entered the roost, the line that best fits the individual plot points shows a slightly greater slope (1.32) than that for the plot of sunset time (0.91). The overall seasonal timing of roosting may be related to the time of sunset, but the day-to-day variation in the time the first birds arrive at the roosting site and enter the roost is greatly influenced by the daily amount of solar radiation impinging on the birds. The termination of roosting events is similarly related to the time when light intensities reach low levels during twilight.

Figure 2 shows the relationships of average daily temperature to solar

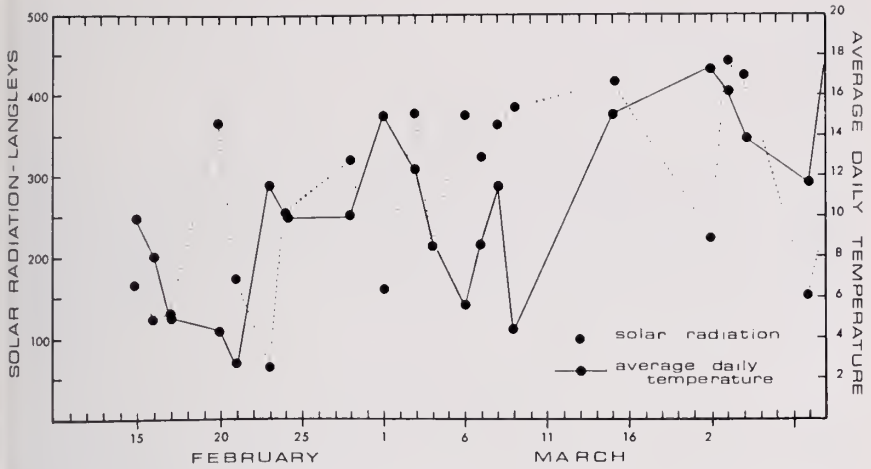

FIG. 2. Plots of average daily temperature (in degrees Celsius) in relation to the amount of solar radiation. The points represent the 21 days on which roosting data were acquired.

radiation. On warm days in winter, cloud cover increases while the amount of solar radiation decreases. In contrast, on cold days the weather is influenced by cold anticyclonic weather systems, the sky is generally clear, and the amount of solar radiation reaching the ground is high. Thus in winter in the Piedmont of South Carolina, the days with relatively high totals of solar radiation are the coldest; the days with relatively low daily totals of solar radiation are the warmest.

DISCUSSION

Light intensity, temperature, cloud cover, and time of sunset have been viewed as influential factors affecting the timing of roosting behavior in birds (Davis 1955), but these factors are interrelated and interdependent (Bliese 1955). Kluijver (1950) found that weather conditions had little influence on the time of roosting although the coefficients for cloudiness were about −0.3. Light intensity and cloudiness have usually been the main factors correlated with roosting behavior (Bliese 1955), but some workers have pointed out that roosting birds forage longer (roost later) on cold days than on warm days (Radford 1954, Davis 1955), and this has advantages from an energetic standpoint. While these explanations are reasonable, there has been little attempt to discuss how the factors interrelate. The data we have gathered suggest a close relationship between the amount of solar radiation and the time birds stop foraging and begin their roosting behavior. The

effects of temperature on roosting behavior may be indirect because the total daily solar radiation is inversely related to the average daily temperature. Moreover, the influence of the daily totals of solar radiation on the duration of activity periods follows the circadian rule (Aschoff 1960).

The circadian rule predicts that for a day-active species in constant conditions, an increase in light intensity will cause the organism to become more active during longer activity periods. Aschoff (1965, 1967) found that this influence also operated in cases of natural entrainment by photoperiod, and that the entrained organisms integrate more or less over the light intensities in both parts of a light cycle. We feel that the timing of roosting in day-active birds functions similarly; that is, the brighter the day (more solar radiation), the later the birds start towards the roost. This relationship would also explain the influence of cloud cover and light intensity reported by other workers. Nice (1943) found that the last evening song of Song Sparrows (*Melospiza melodia*) occurred 13 to 14 min after sunset on clear days and 3 min after the time of sunset on cloudy days, and Dunnett and Hinde (1953) found that Great Tits (*Parus major*) roosted earlier on cloudy days. It would appear then that the total daily amount of solar radiation reaching a bird during the course of a day is an important factor in determining its total behavioral energy budget, and this in turn regulates its activity cycle.

If the amount of solar radiation is an important factor in determining when foraging birds start toward their roost, what factor is responsible for the timing of the final events of roosting? Ambient light intensity after sunset appears to be responsible. Bünning (1973) has pointed out that light intensities during sunrise or sunset are too variable to serve as discrete reference points regulating activity rhythms, because the fluctuations of the light intensities during these phases of the solar day are much too great from day to day, depending especially on cloudiness. He found most suitable as reference points the values of light intensities between about 1 and 10 lux, occurring shortly before sunrise and soon after sunset. In this range of light intensity, the rates of intensity changes are the greatest, and the variations in time because of weather conditions usually do not exceed a few minutes. Bünning thinks an abrupt increase or decrease in intensity is more effective in controlling a physiological process than a gradual one. Our data support Bünning's postulate, for the variation in the times the last birds entered the roost is considerably less than the variation in the times the birds arrived in the vicinity of the roost.

The influence of changing photoperiods or varying daylengths on seasonal behaviors and physiological events is well documented. We suggest that the changing duration and quality (intensity) of light during the day might well

have an equally important effect on the daily behavioral and physiological functions of animals in the wild.

SUMMARY

The timing of Brown-headed Cowbird (*Molothrus ater*) roosting behavior on 21 evenings during February and March, 1972, in the Piedmont of South Carolina was compared to the total daily amount of solar radiation, the time of sunset, and the ambient light levels during twilight. The movement of birds toward the roosting area was closely associated with the total daily amount of solar radiation, while the termination of roosting was more closely correlated to light intensity levels following sunset. The timing of roosting behavior in relation to the quantity and quality of light was in accordance with the circadian rule.

ACKNOWLEDGMENTS

A portion of this work was supported by a grant from the United States Air Force Office of Scientific Research (AFOSR 71-1974). We also wish to thank Brina Kessel for some helpful suggestions.

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DEPT. OF ZOOLOGY, CLEMSON UNIV., CLEMSON, SC 29631. ACCEPTED 28 AUG. 1974.

SOME ASPECTS OF THE BREEDING BIOLOGY OF THE UPLAND SANDPIPER IN NORTH DAKOTA

KENNETH F. HIGGINS AND LEO M. KIRSCH

The general nesting range of the Upland Sandpiper (*Bartramia longicauda*), formerly called Upland Plover, extends from northwestern Alaska, northern Yukon, southern Mackenzie, central Manitoba, southern Ontario, and southern Quebec south into the United States as far as Maryland, Virginia, Kentucky, Oklahoma, and Colorado then north-northwest to northern Oregon. Elliott Coues (1874:504) stated, "Its breeding habits may be studied with perfect success in Northern Dakota, where it is the most abundant of all the waders." As late as 1914, North Dakota was still one of the principal breeding areas for the Upland Sandpiper in the U.S., and only in southern Manitoba and eastern Saskatchewan could breeding pairs of this species be found in greater abundance (Cooke 1914:283). In 1967, Stewart and Kantrud (1972) surveyed the breeding birds of North Dakota and found that the Upland Sandpiper was still a major breeding species there.

The purpose of this paper is to provide a better understanding of certain aspects of the breeding biology of Upland Sandpipers in North Dakota.

STUDY SITE

Data on Upland Sandpipers were collected from 1966 to 1973 at the Woodworth Study Area, a field station of the Northern Prairie Wildlife Research Center located on the Missouri Coteau in northwestern Stutsman Co., North Dakota. The area was about 85% grasslands and 15% croplands and Upland Sandpipers nested mainly on the grasslands. We found nests by searching fields with a 53.35 m cable-chain device similar to that described by Higgins et al. (1969b).

The unplowed grassland is mixed-grass prairie with native dominants of *Agropyron trachycaulum*, *Koeleria cristata*, *Stipa comata* and *S. viridula*. This grassland is heavily infested with two shrubs, *Symphoricarpus occidentalis* and *Elaeagnus argentea* and invaded by exotic cool-season grasses such as *Poa pratensis*, *Bromus inermis* and *Agropyron repens*. The plowed grassland has been seeded with various grasses such as *Agropyron intermedium*, *A. elongatum*, *A. cristatum*, plus alfalfa (*Medicago sativa*) and sweet clover (*Melilotus* sp.). Vegetation commonly used as nesting cover by Upland Sandpipers in this area was reported by Higgins et al. (1969a).

TIME OF NESTING

Arrival on the nesting grounds.—Upland Sandpipers usually arrived at Woodworth during the first 10 days of May although in 1971, they were recorded as early as 22 April. May 5 was the most common arrival date. Lindmeier (1960) reported that Upland Sandpipers arrived in Mahnomen

Co., Minnesota between 1 and 6 May. Mahnomen Co., Minnesota lies about 241 km due east of Woodworth. Roberts (1932) reported arrival dates from 20 April to 10 May in northern Minnesota, averaging 4 May, and from 7 to 25 April in southern Minnesota, averaging 20 April. Upland Sandpipers arrived at the Faville Grove study area in Wisconsin (Buss and Hawkins 1939) approximately 20 days earlier on the average than at the Mahnomen Co. and Woodworth areas. The Faville Grove area lies at a latitude about 515 km south of the other two areas.

Most Upland Sandpipers were segregated into definite pairs upon arrival at Woodworth; some were observed in trios. We did not determine the sex composition of these trios or the length of time they remained intact. Rowan (1926) observed trios of Upland Sandpipers in Alberta, and collected all members of two of these groups, both of which included two males. He stated that groups of three were more common than pairs during 1924 at Sullivan Lake, Alberta, and that no sign of quarreling was noted among members of the trios.

The nesting period.—Nesting activities began at Woodworth as early as 14 days after we saw the first Upland Sandpipers on the area. The earliest clutch recorded was initiated on 17 May, and the latest on 25 June: the mean initiation date of first clutches was 25 May. Buss and Hawkins (1939) noted that nesting began 15 to 20 days after the first sandpipers arrived at Faville Grove. Coues (1874:504) reported that the eggs are mostly laid by the second week of June in northern Dakota.

The earliest hatching of Upland Sandpipers observed at Woodworth was on 14 June and the latest on 22 July. The first major period of hatching was 16 June to 1 July, the peak being around 23 June (Fig. 1). Renesting by Upland Sandpipers may explain the second period of hatching from 7 to 21 July (Fig. 1).

The maximum period between the earliest initiated and the latest hatched nest at Woodworth was 67 days. This agrees closely with the period of not more than 2 months reported by Buss and Hawkins (1939).

The initial nesting effort of Upland Sandpipers appeared to occur almost simultaneously at Woodworth. This is indicated by the sharp rise and peak in initial hatching shown in Figure 1. Further evidence of almost synchronized nesting was observed during 1971 when seven nests hatched between 23 and 25 June. Buss and Hawkins (1939) concluded from their 1937 and 1938 hatching data that Upland Sandpipers begin nesting almost in unison. Goodpaster and Maslowski (1948) found two nests on the same day that were about 180 m apart and both contained two eggs, indicating that these nests were initiated at about the same time.

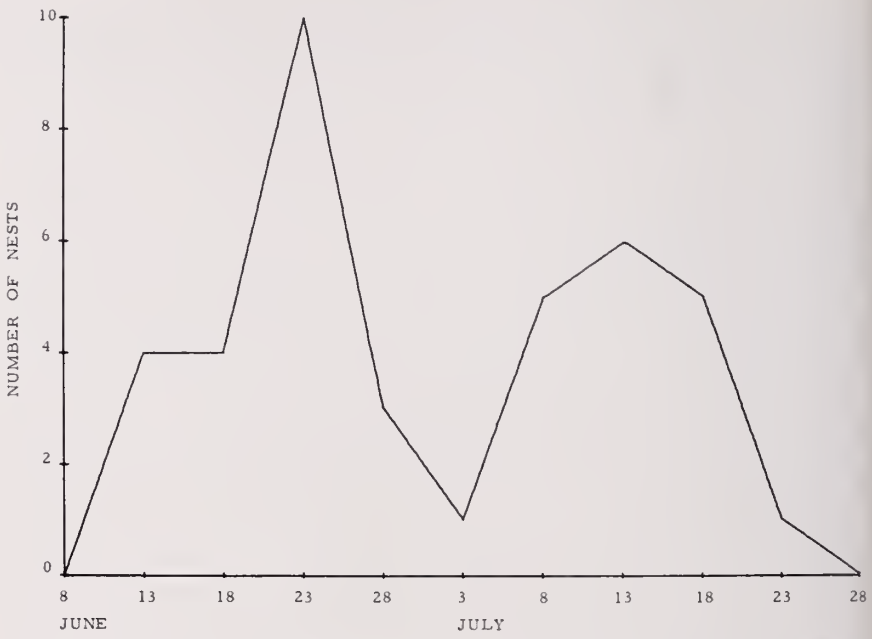

FIG. 1. Distribution of hatching dates for Upland Sandpiper clutches at Woodworth.

EGG LAYING, INCUBATION, AND HATCHING

Egg laying and clutch size.—We determined that the time period between successive laying of individual eggs on three occasions was 24, 29, and 33 hours. A fourth clutch increased from one to four eggs in 79 hours, averaging 26.3 hours between eggs.

According to Bent (1929), this species lays four eggs, rarely five, and perhaps sometimes only three. All of 189 completed clutches at Woodworth consisted of four eggs. Two nests had three-egg clutches for a short time, but neither clutch was confirmed as complete. One of the nests, contained three Upland Sandpiper eggs and one Brown-headed Cowbird (*Molothrus ater*) egg, and was destroyed by a predator before it was again inspected. Higgins (1971) reported a nest near Woodworth with three Upland Sandpiper eggs and one Cowbird egg in which the Upland Sandpiper eggs hatched. The other nest contained three eggs at 11:55 on 1 June and at 17:30 on 3 June, an interval of 53.5 hours; it had been destroyed before a third inspection on 5 June. During three visits to this nest before it was destroyed, an adult bird was flushed from the nest each time, indicating possible incubation of the three eggs and suggesting that the clutch was completed. However, we lacked evidence to confirm that the clutch was previously unaltered and did not record it as a completed three-egg clutch.

One nest of four eggs at Woodworth on 23 June 1970 had only three eggs on 10 July. This clutch had hatched by 15 July. Another nest contained two eggs on 1 June, three eggs on 3 June, four eggs on 5 June, and only three eggs on 22 June. This nest was destroyed by a predator. The disappearance of eggs from these two nests could not be explained. In 1938, Buss and Hawkins (1939) observed a nest that contained four eggs from 26 May to 4 June but only three eggs on 5 June. Incubation was continued on this nest, but no explanation was found for the disappearance of the egg.

Incubation period.—Published reports on Upland Sandpipers show incubation periods as follows: 17 days (Forbush 1929:448; Bent 1929:59), 21 days (Grant 1931:10; Buss and Hawkins 1939:210), 24 days (Bailey 1930:181), 23–24 days (Lindmeier 1960:7), 26 days (Goodpaster and Maslowski 1948:188).

By defining the incubation period as the time from the laying of the last egg in a clutch to the hatching of the last young when all eggs in the clutch hatch (Nice 1954:173; Kendeigh 1963:453) we found that incubation periods for nine clutches ranged from 22 to 27 days (mean = 24 days). Likewise and in accordance with the definition, incubation periods for 12 clutches in the published records cited above ranged from 21 to 28 days (mean = 24 days).

Five clutches at Woodworth did not meet the terms of the definition because one egg in each clutch did not hatch. The incubation period range for these clutches was from 24 to 26 days, and the mean was 25 days, 1 day longer than the normal incubation period, indicating a prolonged effort to hatch all of the eggs. Further evidence of prolonged incubating behavior was noted in 1973 when a four-egg clutch found on 7 June was still being incubated on 8 July, a period of at least 32 days. All four of these eggs contained dead embryos, about two-thirds developed.

Hatching.—At Woodworth, the combined pipping and hatching period for 12 clutches was less than 24 hours at one nest, between 24 and 48 hours at seven nests, and between 48 and 72 hours at four nests. Buss and Hawkins (1939) found the pipping period varied from 18 hours to 3 days and averaged about 24 hours. They also found that the eggs of a given clutch did not pip or hatch simultaneously. Other records for pipping and hatching are as follows: one clutch, less than 24 hours (Bailey 1930), one clutch, nearly 3 days (Grant 1931), two clutches, 2 and 3 days (Goodpaster and Maslowski 1948).

Egg hatching success was determined from 100 clutches containing four eggs each that did not suffer losses from predation and were incubated long enough to have hatched. Of 400 eggs observed, 377 (94%) hatched and of the 23 eggs that did not hatch, 15 were rotten and 8 had dead embryos. Four of the rotten eggs were in one clutch and four of the dead embryos were in another clutch; both clutches were found in 1973, an extremely dry year

for nesting. In 10 other clutches only three eggs hatched per clutch and in one clutch only two hatched. Of 104 eggs that Buss and Hawkins (1939) observed, 101 (97%) hatched. They determined that the three unhatched eggs were infertile.

Characteristics of a hatched clutch.—Because the shells of hatched eggs are usually carried away by the attending adult as the chicks hatch, it is difficult to determine whether or not an Upland Sandpiper clutch hatched from the appearance of the nest remains. We found in at least 75% of the 98 hatched clutches we inspected, the nest remains were shallow bowl-shaped depressions, containing few to very many minute egg shell chips and very little vegetative litter. Pipped egg shells with attached membranes were found at eight nests. Two other nest bowls contained no discernible shells or shell chips, although the eggs were known to have hatched. A newly hatched chick was present in one of these nests, and two pipped egg shells with membranes attached were found within 16 m of the other. Buss and Hawkins (1939) found that shells had disappeared from 54% of the hatched nests in their study, evidently carried away by the incubating bird.

FALL DEPARTURE

Coues (1874:505) reported that Upland Sandpipers left the northern regions early and that he saw none after early September. During most years, a majority of Upland Sandpipers have left the Woodworth area by 25 August. We have only two records for latest departures: 22 August 1972 and 3 September 1973.

During 1972 and 1973, Upland Sandpipers were present at Woodworth for periods of 110 and 122 days, respectively. Between their arrival and departure, we surmised, conservatively, that at least 110 days are required to complete their breeding ground activities. During 1935–1938, Buss and Hawkins (1939) found that Upland Sandpipers were present at Faville Grove for periods ranging from 114 to 165 days and a mean of 138 days. Their data showing a longer period than for Woodworth, are reasonable because of the longer growing season at Faville Grove. The average period free of killing frost at Pettibone, the nearest long-term weather station to Woodworth, was 109 days, extending, on the average, from 27 May to 13 September (Kincer 1941:1045). The average period free of killing frost at Lake Mills, the nearest long-term weather station to Faville Grove, was 152 days, and, on the average, this period extended from 8 May to 7 October (Kincer 1941:1192). These dates nearly coincide with the dates for first nest initiation and final departure dates for Upland Sandpipers on the two study areas, indicating that some of their breeding ground activities may be directly or indirectly correlated with temperature at these northern latitudes.

SUMMARY

Observations of certain aspects of the breeding biology of Upland Sandpipers were made from 1966 to 1973 on the Woodworth Study Area in east-central North Dakota. After arriving on the area Upland Sandpipers completed their breeding ground activities and departed after a period of 110 to 122 days. first arrivals were usually seen around 5 May, and in most years no birds were seen after 25 August. The maximum period from the earliest clutch initiation until the latest hatch was 67 days. The average time lapse between the laying of any two eggs is probably between 24 and 36 hours. All clutches known to be complete contained four eggs. The mean incubation period was 24 days, and all eggs in any one clutch completed pipping and hatched within a period of 1 to 3 days. Egg hatching success for 400 fully incubated eggs was 94%. The appearance of a completely hatched clutch was most commonly a shallow, bowl-shaped depression containing few to many minute egg shell chips and very little vegetative litter.

ACKNOWLEDGMENTS

We thank Dr. I. O. Buss, H. W. Miller, T. J. Dwyer, R. E. Stewart and P. F. Springer for reviewing the manuscript. We also thank the several seasonal employees for assisting with the collection of field data.

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Northern Prairie Wildlife Research Center, U.S. Fish and Wildlife Service, Jamestown, ND 58401. Accepted 20 Aug. 1974.

NEW LIFE MEMBER

Mr. Frank B. Smithe has recently become a life member of the Wilson Ornithological Society. Mr. Smithe has a degree in mechanical engineering from Columbia University and he is presently retired from his profession, though he is quite busy with his avocation—bird conservation. Mr. Smithe is the author of "Birds of Tikal" and (soon to be published) "A Naturalist's Color Guide." For several years Mr. Smithe served as treasurer of the International Committee for Bird Preservation; he is an elective member of the AOU, and is active in many other conservation and ornithological organizations. Mr. Smithe has one son and three granddaughters.

GENERAL NOTES

***Ichthyornis* in the Cretaceous of Alabama.**—Apart from *Archaeopteryx* and *Hesperornis*, *Ichthyornis* is perhaps the most famous of fossil birds. It is the sole genus of the Ichthyornithidae, of which O. C. Marsh named six species from the Smoky Hill Chalk, Niobrara Formation, of the Upper Cretaceous of Kansas, and a seventh from the Upper Cretaceous Austin Chalk of Texas (for a list of species see Brodkorb, Bull. Fla. State Mus. Biol. Sci. 11:99–220, 1967). For a time there was controversy (summarized in Brodkorb, p. 19–55, *In* Avian Biology, vol. 1 [Farner and King, eds.], Academic Press, New York, 1971) over whether *Ichthyornis* actually possessed teeth, as Marsh (Odontornithes: a monograph of the extinct toothed birds of North America. U.S. Geol. Expl. 40th Parallel Vol. 7, Govt. Printing Office, Washington, D.C., 1880) had supposed, but the evidence now seems to indicate that it did (Russell, Peabody Mus. Nat. Hist. Yale Univ. Bull. 23:121, footnote, 1967; Gingerich, Condor 74:471–473, 1972). The Ichthyornithidae and another Cretaceous family, the Apatornithidae, form the order Ichthyornithiformes, which Brodkorb (1967) places near the Charadriiformes.

Another Upper Cretaceous bird, *Plegadornis antecessor* Wetmore (Smithson. Misc. Coll. 145[2]:1–17, 1962), was described from the distal end and part of the shaft of a humerus from the Mooreville tongue of the Selma Chalk in Alabama. Wetmore assigned this fossil to a new family, Plegadornithidae, which he placed near the ibises (Threskiornithidae) in the order Ciconiiformes. Recently, Kashin (Ornitologiya 10:336–337, 1972) has pointed out that the name *Plegadornis* Wetmore 1962 is preoccupied by *Plegadornis* Brehm 1855, a synonym of *Plegadis* Kaup 1829. He substituted the new names *Angelinornis* and Angelinornithidae for Wetmore's *Plegadornis* and Plegadornithidae, respectively.

Because *Angelinornis* is roughly contemporaneous with *Ichthyornis*, I undertook a comparison of the two genera. One of the difficulties inherent in this is that most of the specimens of humeri of Marsh's species of *Ichthyornis* are crushed, flattened, and essentially two-dimensional. All comparisons I made of *Angelinornis* with *Ichthyornis* were with a well-preserved distal end of a humerus of *Ichthyornis* (YPM 1764) from the Smoky Hill Chalk. This specimen is almost identical in size to the type of *A. antecessor* (the distal width of both specimens is 10.5 mm). It is intermediate in size between the measurements given by Marsh (1880) for *I. dispar* and *I. victor* but its dimensions are close to those of another specimen (10.3 mm) referred to *I. dispar* by Brodkorb (pers. comm.). I therefore refer YPM 1764 to *I. dispar* pending Dr. Brodkorb's revision of *Ichthyornis*.

The type humerus of *A. antecessor* is extremely similar to the humerus of *I. dispar* (Fig. 1). It has the following features in common with *Ichthyornis*: prominent, truncate ectepicondylar process located rather high on the shaft with a distinct pit at its proximal base; internal and external condyles on about the same distal plane; entepicondyle weak, lying proximal to the internal condyle; entepicondylar prominence well-developed; a deep square depression on the palmar surface bounded by the entepicondylar process, internal condyle, and external condyle; brachial depression shallow; shaft not markedly curved; olecranal fossa shallow and ill-defined; external condyle with a large nutrient foramen at its proximal apex; and tricipital grooves very indistinct. Although the humeri of both *Angelinornis* and *Ichthyornis* bear a superficial resemblance to those of

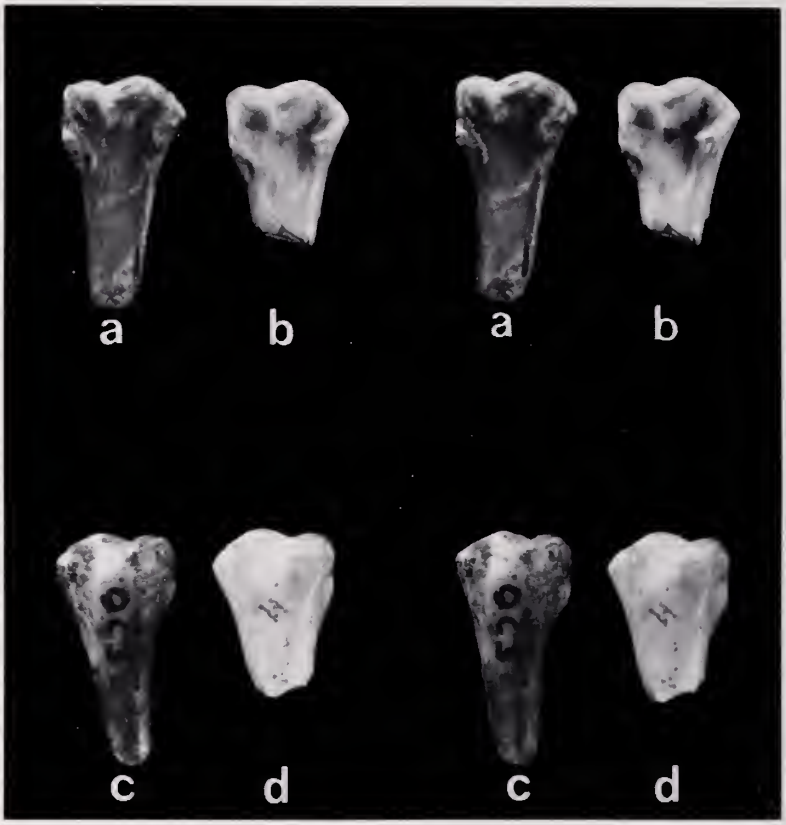

FIG. 1. Stereophotographs of distal ends of humeri of *Ichthyornis*, 1.5 × (palmar view in upper row, anconal view in lower). *a* and *c*, holotype of *I.* ("*Angelinornis*") *antecessor* USNM 22820. *b* and *d*, *I. dispar* YPM 1764.

the Phaethontidae, Threskiornithidae, Burhinidae, and the Cretaceous Telmatornithidae, the above combination of characters distinguishes them from any of these families. Harrison (Bull. Br. Ornithol. Club 93:123–126, 1973) has shown that the proximal end of the humerus of *Ichthyornis* is totally different from that of all other known birds, but unfortunately this part is lacking in *Angelinornis*.

Although the humerus of *Angelinornis antecessor* shows some differences from that of *I. dispar*, I can find nothing in its features that will permit its separation from *Ichthyornis* at the generic level. The differences between *Angelinornis* and *Ichthyornis* are no greater than the intrageneric variation observed within modern taxa of birds. Therefore, I recommend that *Angelinornis* be synonymized with *Ichthyornis*, and that Angelinornithidae be synonymized with Ichthyornithidae.

The type humerus of *I. antecessor* may be distinguished from that of *I. dispar* as follows: shaft not as heavy, brachial depression shallower and located slightly more

distally, ectepicondylar process more prominent, and the pit at the base shallower. There appear to be some differences in the attachment for the anterior articular ligament, but this area is much abraded in the type of *I. antecessor*. In anconal view the two species are virtually inseparable except for the difference in the robustness of the shaft. The type of *I. antecessor* is clearly specifically distinct from the specimen here referred to *I. dispar*. Since the other species in the genus are reported to be either larger or smaller than these specimens, it seems most probable that *antecessor* is a valid species of *Ichthyornis*.

I am most grateful to Pierce Brodkorb for permitting me to examine the specimen of *Ichthyornis dispar* from the Peabody Museum, Yale University (YPM) while it was in his care, and for his discussions of the manuscript. John Farrand, Jr. and Robert J. Emry also read and commented on the manuscript. The photographs are by Victor E. Krantz, to whom my thanks are due.—Storrs L. Olson, *National Museum of Natural History, Smithsonian Institution, Washington, DC 20560.* *Accepted 3 July 1974.*

Notes on nests of four avian species from the Coastal Cordillera of Venezuela.—Breeding seasons and nest sites of many Neotropical bird species are generally so poorly known that comparison of reproductive strategies is difficult. These observations from the Coastal Cordillera of Venezuela east of Colonia Tovar in the Federal District, and Rancho Grande (Parque Nacional Henri Pittier), Aragua, are reported to contribute additional data on the nesting of three species, the Golden-crowned Flycatcher (*Myiodynastes chrysocephalus*), Cinnamon Flycatcher (*Pyrrhomyias cinnamomea*) and Slate-throated Redstart (*Myioborus miniatus*), and to present the first nesting account of the Black-capped Tanager (*Tangara heinei*). The six nests reported here were located at clearing edges resulting from road cuts and forest destruction on generally forest-covered mountain slopes in the subtropical zone. The nests found were within the elevation ranges listed for these species in Venezuela by Phelps and Phelps (Bol. Soc. Venez. Cienc. Nat. 24(104–105):1–479, 1963). The breeding dates supplied in this note confirm the nesting seasons of these species hypothesized by Schäffer and Phelps (Bol. Soc. Venez. Cienc. Nat. 16:3–167, 1964) at Rancho Grande and augment the sparse literature on nest sites and breeding seasons of Neotropical birds.

Myiodynastes chrysocephalus.—A nest found 18 May 1969 in an area of tall, lower subtropical forest at about 1360 m in the state of Aragua near Colonia Tovar probably contained young as both parents were carrying food to the nest. The nest was about 12 m above the road in a protected niche on a ledge of a vertical outcrop. The nest was not accessible for closer examination.

Other accounts of nesting *M. chrysocephalus* or its close ally, *M. hemichrysus*, are few. Michael Gochfeld (pers. comm.) located a bulky, largely moss-constructed, cup-shaped nest of *hemichrysus* in Costa Rica on 9 May 1969 and Skutch (Pac. Coast Avif. 34:1–593, 1960) found two nests of *hemichrysus* in Costa Rica about 23 m and 30 m above ground in niches among arboreal mosses and epiphytic roots.

Pyrrhomyias cinnamomea.—One nest was found 17 May 1969 in the Federal District near Colonia Tovar at approximately 1700 m in subtropical forest. The cup-shaped nest was about 1.5 m up a 3 m high road cut in a recess just large enough to hold the largely moss constructed nest. It contained two white eggs blotched with reddish-brown. Another Cinnamon Flycatcher, presumably its mate, appeared after the incubating bird was flushed from the nest in late afternoon. Gochfeld (pers. comm.) located another nest 30 April 1970 at Rancho Grande at 1000 m. This bulky nest, made of moss and

camouflaged with tree bark, was on a dead stub of a living tree. Nest contents were not known but incubation apparently had begun.

A photograph of a pair at a nest in "A Portfolio of Venezuelan Birds" by Paul Schwartz (undated publication of the Cornell Laboratory of Ornithology) further implicates crevices in banks as important nest sites of Cinnamon Flycatchers. In notes accompanying the photograph Schwartz wrote that "Cinnamon Flycatchers frequently nest in niches along roadsides."

Myioborus miniatus.—An adult was flushed from a nest on 17 May 1969 in the Federal District near Colonia Tovar at approximately 1700 m. The nest, constructed of dried herbs and grasses, was about 1 m above a dirt trail in a recess on the same bank as the 1969 *Pyrrhomyias cinnamomea* nest and contained two white eggs finely dotted with reddish-brown. The nest was partially concealed by overhanging ferns and other plants, which gave the nest a dome-like appearance. Gochfeld (pers. comm.) found a nest at Rancho Grande on 29 April 1970 at 1000 m. This nest was about 1 m above a path in a cavity on a vertical cut bank. The entrance was overhung by mosses. The nest held three eggs.

Slate-throated Redstart nest sites in Central America are similar to these Venezuelan sites. Skutch wrote "The oven-shaped nest was most often placed in a niche in a cut bank" (Pac. Coast Avif. 31:369, 1954). He also reported clutch sizes of two to three.

Tangara heinei.—A female was observed carrying herbaceous material to a partially constructed nest being built on an isolated, sparsely-leaved 1 m tall shrub on a steep, moss-covered slope. I observed the birds for about one hour at 1360 m in Aragua near Colonia Tovar on 18 May 1969. Only the female carried nesting material but both male and female molded the material into the nest. This appears to be the first published nesting account of this species.

I thank Eugene Eisenmann, Michael Gochfeld, Wesley E. Lanyon, William H. Phelps, Jr. and Paul Schwartz for critically reading the manuscript. The observations were made incidental to studies supported by the L.C. Sanford Trust Fund of the American Museum of Natural History.—David Ewert, *Dept. of Ornithology, American Museum of Natural History, Central Park West at 79th St., New York, NY 10024.* *Accepted 2 July 1974.*

Incubation by a male Fulvous Tree Duck.—On 26 July 1968, I obtained evidence of a male Fulvous Tree (Whistling) Duck (*Dendrocygna bicolor*) incubating 13 eggs near El Campo, Wharton Co., on the Texas Gulf Coast.

I observed two Fulvous Tree Ducks (sexes indistinguishable by plumage) fly from a nest near the edge of a rice field and then return a short time later. One of the birds settled on the nest and remained, while the other circled and left. I collected the bird on the nest, and on dissection, found it to be an adult male. Three eggs examined from the clutch contained 18-day-old embryos.

Bolen (J. Wildl. Manage. 35:385–388, 1971) reported that wild male Black-bellied Tree Ducks (*D. autumnalis*) share incubation duties with their hens, but to my knowledge, this behavior has not been confirmed for wild Fulvous Tree Ducks. Delacour (The waterfowl of the world, vol. 1, Country Life, Ltd., London, 1954) suggested that male Fulvous Tree Ducks share in incubation, possibly even performing most of it, and contribute as much as the females in looking after the young. Meanley and Meanley (Wilson Bull. 71: 33–45, 1959) also suggested that both male and female Fulvous Tree Ducks share in most phases of nesting activity. However, many life history descriptions of this species have not reported incubation by the male (e.g., Bent, U.S. Natl. Mus. Bull. 130, 1925; Kortright, The

ducks, geese and swans of North America, Stackpole Co. and Wildl. Inst., Harrisburg, Pa., 1942; McCartney, The Fulvous Tree Duck in Louisiana, Louisiana Wildl. and Fisheries Comm., New Orleans, 1963). My observation confirms that wild male Fulvous Tree Ducks, like male Black-bellied Tree Ducks share incubation.—Edward L. Flickinger, *U.S. Fish and Wildlife Service, Victoria, TX 77901. Accepted 15 July 1974.*

Cases of birds reducing or eliminating infestations of tobacco insects.—The tobacco hornworm (*Manduca sexta*) and tobacco budworms (*Heliothis virescens* and *H. zea*) commonly attack growing tobacco and are controlled by chemicals. I have observed that birds sometimes eliminate or substantially reduce local infestations of these insects. Six such cases are here reported, involving six species of birds. These observations were made near Oxford, Granville Co., North Carolina, during the summer of 1972.

I made observations between 05:00 and 09:00 and between 17:00 and 21:00. The food of the birds was usually determined in the field with aid of 7×35 binoculars and knowledge of where the birds were feeding. Some birds were collected and contents of their digestive tracts examined using a stereomicroscope. I made counts of larval populations to determine the extent of infestations and predatory activities of birds and approximated ages of larvae from sizes of fecal pellets and areas of leaf damage.

On 3 July I saw three Common Crows (*Corvus brachyrhynchos*) walking in a 1.2 ha tobacco field. I examined 200 plants in various parts of the field; 16 (8%) had hornworm damage. I found two larvae, both in the early fifth instar, which I moved to plants I could easily watch from concealment. On the second day of watching I saw a crow remove one larva. I found no hornworm larvae reaching the prepupal stage in this field. This field was surrounded by woodland, and the three crows remained nearby throughout the 1972 growing season. The crop received no chemical treatment for insect control, and the farmer was satisfied with his yield.

On 26 July I found two Mockingbirds (*Mimus polyglottos*) feeding on tobacco hornworm larvae in an 0.8 ha tobacco field. Examination of 200 plants revealed that 36 (18%) had hornworm damage. Larvae were gone from 17 of the 36 (47%) plants. Judging from the extent of damage the larvae were removed chiefly at the earlier stages of growth. This tobacco was treated with insecticide on 27 July, thus terminating my study. The field was next to a farmstead and nearby nesting habitat for Mockingbirds.

On 24 August I saw four Eastern Bluebirds (*Sialia sialis*) feeding on tobacco budworm larvae near the edge of a 1.8 ha tobacco field. In the area adjacent to that where the birds were foraging, 32 of 100 plants had larvae in their seed heads. In the area where the birds were foraging, 14 of 100 plants contained larvae. Damage to the plants provided evidence that additional larvae had been present. Thus, the larvae had been removed from 18 of 32 (56%) plants. The larvae were in the third or later instars.

House Sparrows (*Passer domesticus*) were seen foraging on tobacco plants on 5 July. I was unable to find a single larva in the 0.6 ha tobacco field, though six of eight nestling House Sparrows collected from nearby nests had one or two hornworm larvae in their digestive tracts. The nine larvae found in these birds were all small, in the second or late first instar. There were old buildings suitable for use by House Sparrows on three sides of the tobacco field, and 11 nests were found. This field was not treated with insecticides, and it received no detectable damage from insects.

A local farmer reported to me experiences that led him to depend on birds for control of insects on his tobacco. He noted the presence of hornworms on his tobacco late in

a week during the summer of 1968 and made plans to apply insecticide the following Monday. During the weekend he saw a flock of birds in the field, and on the following Monday no hornworm larvae could be found. When I spent 5 hours on the mornings of 2 and 3 August on this farm watching for feeding birds, I saw Red-winged Blackbirds (*Agelaius phoeniceus*) in the field. Fresh larval droppings beneath a plant visited by a Red-wing indicated that there had been an active hornworm larva on the plant a short time earlier. I found no hornworm larvae in an examination of 100 plants. There was a small marsh and a breeding population of Red-winged Blackbirds beside this tobacco field. This farmer annually grows 4–6 ha of tobacco, and he has used no insecticide on tobacco since he saw the birds in 1968.

On 29 June I saw a small flock of Common Grackles (*Quiscalus quiscula*) fly from a tobacco field. Two of them carried large hornworm larvae. In a search of the tobacco field, I found no hornworm larvae, though 27 of 150 (18%) plants had leaf damage and below that hornworm droppings, indicating that larvae had grown on the tobacco to the fourth and fifth instars.

In a previous study, Stewart (J. Econ. Entomol. 62:956–957, 1969) reported removal by House Sparrows of all of 2000 tobacco hornworm larvae not earlier falling to the ground after they had been placed on the plants in an attempt to rear them. Similarly, Thurston and Prachuabmok (J. Econ. Entomol. 64:1548–1549, 1971) indicated that most larvae were removed by Common Grackles after the larvae had been placed on tobacco plants in tests of bird predation.

There have also been reports of birds making substantial contributions toward control of insects attacking corn. One of these involved the destruction during the winter by Common Flickers (*Colaptes auratus*) of 63.7% of the larvae of southwestern corn borers (*Diatraea grandiosella*) in an area of Mississippi where 54.4% of the stalks were infested (Black et al., Annals Entomol. Soc. Am. 63:701–706, 1970). Stewart (Auk 90:911–912, 1973) reported removal by Starlings (*Sturnus vulgaris*) of all larval corn earworms (*Heliothis zea*) and fall armyworms (*Spodoptera frugiperda*) on corn ears in areas of southcentral Virginia and northcentral North Carolina, with the birds not eating the corn.

In a continuing program of integrated control of insects attacking apples in Nova Scotia orchards, MacLellan (Canad. Entomol. 90:18–22, 1958; Canad. Entomol. 91:673–680, 1959; Proc. Tall Timbers Conf. Ecol. Manage. Animal Cont. Hab. 2:273–284, 1970) has found that Hairy and Downy Woodpeckers (*Dendrocopos villosus* and *D. pubescens*) regularly reduce infestations of codling moths (*Laspeyresia pomonella*) from a potential to a negligible threat.

The recent literature on the role of birds in control of forest insects is much more abundant than that on orchard and field crop insects. Bruns (Bird Study 7:193–208, 1960) reviewed research reports from England, Germany, the Netherlands, Czechoslovakia, and Russia, citing 68 references. Buckner (Ann. Rev. Entomol. 11:449–470, 1966) reviewed research on the role of vertebrates in control of forest insects and cited 109 references.

My experiences reported in this note lead me to think that there may be many unexploited possibilities for management practices using birds in control of undesirable insects. This conclusion is particularly applicable to conditions in North Carolina, where farm crops are often grown in small fields. With tobacco, management practices might include erection of nest boxes for bluebirds, planting crops near farmsteads and nesting populations of House Sparrows, planting crops near a marsh and a nesting population of Red-winged Blackbirds, and planting nesting cover for Mockingbirds. Most im-

portantly, chemical control should be delayed until it is apparent that birds cannot provide the desired degree of insect control.

Research reported on in this note was supported by the Agricultural Research Service, U.S. Dept. of Agriculture. I am grateful to Richard Thurston for helpful comments offered after a reading of an early version of this manuscript.—Paul A. Stewart, *203 Mooreland Drive, Oxford, NC 27565.* *Accepted 24 July 1974.*

Interactions between Forster's Terns and American Coots.—Recently Burger (Wilson Bull. 85:449–451, 1973) documented competition for nest sites and aggression between Franklin's Gulls (*Larus pipixcan*) and American Coots (*Fulica americana*) nesting in a Minnesota marsh. I will present data collected at Delta, Manitoba on interactions between coots and Forster's Terns (*Sterna forsteri*), another larid nesting in the same sort of marsh habitat as Franklin's Gull (McNicholl, M.S. thesis, Univ. Manitoba, 1971). As was the case in Burger's study, several species nested among the larids, but most were never attacked by the tern. Black-crowned Night Herons (*Nycticorax nycticorax*) and American Coots were the only exceptions. The herons were attacked only while attempting to land in the colony (McNicholl, Auk 90:902–904, 1973); the coots were attacked as described below.

The tern colony, situated on seven "islands" of *Scirpus acutus* in a marsh bay, had nests placed on floating vegetation and muskrat (*Ondatra zibethicus*) houses. Coots nested both on solid ground along the edges of the bay and on floating mats on the *Scirpus* "islands." Six coot nests were on the "islands" in 1968 and eight in 1969, but most were not among the tern nests. Of the three that were among tern nests, two were closer to tern nests than the adjacent tern nests were to each other. Thus, coots tended to nest close to but not among terns, but were tolerated at close range by the terns. The selective advantage for the coots of nesting in the vicinity of the terns may be related to predator avoidance, as the terns and Yellow-headed Blackbirds (*Xanthocephalus xanthocephalus*) were efficient at keeping away avian predators (McNicholl 1973) by mobbing them, a behavior not practiced by coots. As these predators were usually kept from the entire bay, this advantage would be imparted to the coots whether or not they nested close to the terns. On the other hand, since coots were attacked if approaching tern nests (see below), it would be advantageous for the coots to nest away from the immediate vicinity of tern nests.

Although coots fed daily in open parts of the bay, I only once saw one attacked there by a Forster's Tern. In this case the tern had attacked the coot near the tern's nest just prior to the attack in the open bay. Similarly terns did not attack coots swimming slowly along the edges of the "island" feeding. However terns always attacked coots either approaching a tern nest directly or swimming in a deliberate manner (charging) toward the "islands." After my daily visits to the tern nest and in about 20 additional observations, coots of the three nests close to tern nests always approached their own nests from the side opposite the tern nest. Usually one tern attacked one coot, but once a coot was attacked by two terns simultaneously, and once by six terns. In two cases two terns attacked two coots simultaneously, that is both terns attacked both coots. Attacks consisted of swoops from above, usually resulting in the coot's either turning away or diving immediately. In one case a coot did not retreat immediately, and was struck several times on the head by the tern. This was the only case in which a tern actually struck a coot on the water. Once a flying coot was struck on the head and legs by a tern. This was the only case of an attack on a flying coot.

There may be at least three advantages to terns in keeping coots away from nests or young. The use of similar nesting substrates makes coots potential nest site competitors (see below and Burger 1973). The clumsy manner in which coots land and take off, especially if frightened, may make their mere presence near a nest dangerous. Burger (1973) twice observed coots preying on gull eggs in Minnesota and reported other observations of egg predation by coots. In addition Lawrence (Chickadee Notes No. 595. Winnipeg Free Press, 4 Aug. 1932) reported a coot drowning a downy Canvasback (*Aythya valissineria*), and later (Chickadee Notes No. 796, Winnipeg Free Press, 26 June 1936) suspected them of killing young Franklin's Gulls, and Collins (Auk 61:299, 1944) observed a coot drowning a downy Mallard (*Anas platyrhynchos*).

Although coots have been observed to use muskrat houses for loafing, copulating, and brooding in other areas (Fredrickson, Wilson Bull. 82:445–457, 1970), on Forster's Bay they used only floating mats of dead *Scirpus* for these activities, and only those not used by terns for courtship or maintenance activities. This was true even in 1969 when several muskrat houses were not used for nesting by terns. The terns used all these structures for courtship activities before either the terns or coots were nesting, and this may have discouraged the coots from using them. This contrasts with Burger's observations on Franklin's Gulls in which approaching coots usually caused gulls to leave such sites, and occasionally coots even charged the gulls. I never observed a coot attack or threaten a tern, but Van Rossem (Condor 35:49–51, 1933) saw a coot chase a Forster's Tern away from the vicinity of the coot's nest, and Ryder (Auk 76:424–442, 1959) included Forster's Tern among birds threatened by coots when near coot young. As Forster's Terns have been reported to prey on eggs (Van Rossem 1933), it may be to the coot's advantage to keep the terns away.

Thus, a complex situation involving potential competition for nest sites, protection to coots from predators by nesting among aggressive terns, and potential predation by either species on the other may exist between Forster's Terns and American Coots similar to that reported by Segré et al. (Wilson Bull. 80:213–219, 1968) for Laughing Gulls (*Larus atricilla*) and Clapper Rails (*Rallus longirostris*).

This note constitutes Publication No. 21 of the University of Manitoba Field Station, Delta, Manitoba. Help of many kinds was offered by several people as acknowledged in McNicholl (1971). This manuscript benefited from the comments of C. G. Beer, Joanna Burger, Roger M. Evans, Jack P. Hailman, and Ronald A. Ryder.—Martin K. McNicholl. *Dept. of Zoology, Univ. of Manitoba, Winnipeg, Manitoba (Present address: Dept. of Zoology, Univ. of Alberta, Edmonton, Alberta T6G 2E1).* *Accepted 15 July 1974.*

Mobbing and other interspecific aggression by Barn Swallows.—Hartley (Symp. Soc. Exp. Biol. No. 4:313–336, 1950) defines mobbing as a "demonstration made by a bird against a potential or supposed enemy belonging to another and more powerful species, it is initiated by the member of the weaker species, and is not a reaction to an attack upon the person, mate, nest, eggs, or young." We recognize mobbing as a form of interspecific aggression, but we do not recognize all forms of interspecific aggression as being synonymous with mobbing. Bent (U.S. Natl. Mus. Bull. 179, 1942), Cross (Wilson Bull. 62:39, 1950), Samuel (Wilson Bull. 83:296–297, 1971), and Beason (Inl. Bird-Banding News 46:55–56, 1974) have reported instances of Barn Swallow (*Hirundo rustica*) mobbing behavior or other interspecific aggression directed toward a Sharp-shinned Hawk (*Accipiter striatus*), a Loggerhead Shrike (*Lanius ludoricianus*),

a Cliff Swallow (*Petrochelidon pyrrhonota*), and a Dickcissel (*Spiza americana*), respectively.

We observed interspecific aggression and mobbing by Barn Swallows between 14 May 1973 and 9 June 1974 in a population nesting under concrete and wooden bridges at Sabine National Wildlife Refuge, Cameron Parish, Louisiana.

On separate occasions, interspecific aggression was directed toward a Cliff Swallow and two Bank Swallows (*Riparia riparia*). These two species were harassed by single Barn Swallows when they flew beneath or near a bridge that supported nests containing eggs and or young.

We saw extensive mobbing, involving large numbers of Barn Swallows, directed toward Snowy Egrets (*Egretta thula*) in three separate but similar incidents. In each instance of mobbing, the attack was initiated when the egret approached within 50 to 70 m of the nesting colony. The mobbing was directed to all parts of the egret's body. Two degrees of mobbing intensity were noted: one involved fewer than a dozen birds that alternately attacked the egret, while the other involved most or all members of the colony that simultaneously attacked the egret. The number of Barn Swallows actively participating in mobbing depended on the egret's distance from the bridge. All three incidents of mobbing lasted for approximately one hour. Physical contact between the two species was rare. During the diving attacks by single Barn Swallows, the egret ducked its head but did not show alarm unless a swallow came very close. A hit or near hit by the Barn Swallows stimulated the egret to snap its bill. This peculiar behavior produced a sound that was audible over distances of 30 to 40 m. Although the egret continued to forage at the water's edge, mobbing appeared to greatly diminish its food gathering efficiency. When the egret flew to a new feeding site under the bridge supporting the nesting colony, all members of the colony, including incubating and brooding birds, were summoned by the loud and persistent calls of the birds involved in the original mobbing. The colony's extensive attack was brief and then most of the swallows returned to their previous activities. The small number of birds that persisted alternated their attacks on the egret. In spite of the attacks, the egret wandered at will under the bridge while foraging and continued to duck and snap at the diving swallows.

We flushed an egret from beneath the bridge on two occasions. In each instance, the egret was violently attacked in flight by approximately 15 swallows in a fashion similar to that of a crow (*Corvus* spp.) being mobbed by Blue Jays (*Cyanocitta cristata*). At this time, many direct hits were made to the egret's body and this mobbing continued over a distance of about .75 km. The cause for the mobbing of the egrets was not clear, since both Green Herons (*Butorides virescens*) and Louisiana Herons (*Hydranassa tricolor*) frequently fed under or near the nesting colony, but were never attacked.

An Eastern Kingbird (*Tyrannus tyrannus*) and a male Red-winged Blackbird (*Agelaius phoeniceus*) were each mobbed once by single Barn Swallows as they flew within 10 to 20 m of a swallow colony. Many other Kingbirds and Red-wings flew unmolested near swallow colonies.

Boat-tailed Grackles (*Cassidix major*) were the most frequently mobbed or harassed of all observed species. On every occasion, only males were attacked, perhaps because their singing and plumage displays near bridges made them more obvious than the females. On four different occasions, single Barn Swallows made repeated dives at male Boat-tailed Grackles that had perched near a colony. In two other incidents, mated pairs attacked a grackle that had perched near their newly fledged young. All aggression was directed to the head or upper thoracic region of the grackle, eventually causing it to leave the immediate area. During our study, Boat-tailed Grackles were

never observed to prey on adults, nestlings, or eggs of the Barn Swallow. Bent (U.S. Natl. Mus. Bull. 211, 1958), however, reported that Great-tailed Grackles (*Cassidix mexicanus*) ate eggs and nestlings of other birds. McIlhenny (Auk 54:274–295, 1937) presented no evidence of Boat-tailed Grackle predation on the eggs and nestlings of other avian species in Louisiana.

This study was conducted through the authorization of National Wildlife Refuge Permit No. 4-73-24. We wish to thank Mr. John R. Walther, Refuge Manager, for allowing access to refuge facilities, Dr. Carroll L. Cordes, and Mr. Philip A. St. Romain for constructive criticism of the manuscript.—Harland D. Guillory and Dwight J. LeBlanc, *Dept. of Biology, Univ. of Southwestern Louisiana, Lafayette, LA 70501.* *Accepted 17 Aug. 1974.*

Clapper Rail feeding on water snake.—The ornithological literature makes no reference to reptiles as food of the Clapper Rail (*Rallus longirostris*). On 2 May 1974 I observed a Clapper Rail feeding in a salt marsh ditch about 50 m from open water in Buzzards Bay, Mattapoisett, Plymouth Co., Massachusetts. When I arrived, the bird was throwing from side to side a snake approximately 40 cm in length. I watched the bird for about one minute as it tore the entrails of this specimen. I flushed the bird and found a recently killed water snake (*Natrix sipedon*). Most of the entrails had been removed. I do not know exactly how the snake was killed or if it was killed by the Clapper Rail.—James G. Hoff, *Southeastern Massachusetts Univ., Dartmouth, MA 02747.* *Accepted 2 Aug. 1974.*

An additional record of two Tree Swallow females using the same nest box.—Although the Tree Swallow (*Iridoprocne bicolor*) is normally a monogamous species, Farber (Wilson Bull. 84:204, 1972) reported an apparent case of polygyny in that species and Bent (U.S. Natl. Mus. Bull. 179, 1942) reports several instances of more than two adult Tree Swallows occupying the same nest site.

On 29 May 1974, I encountered a nest of Tree Swallows in a nest box near Washington, Macomb Co., Michigan, which contained 11 eggs. On that date I was able to capture and band three of four birds which remained near and defended the nest box. Two of the four birds were females; both had well-developed brood patches, although one was much duller than the other. A third bird was judged to be a male, as no brood patch was present. The fourth bird, thought to be a male, was more cautious and could not be trapped.

Hatching occurred on 8 or 9 June and was synchronized, since 11 young of about the same size were present on my subsequent visits on 12, 13, and 19 June. However, beginning on 19 June and continuing thereafter, only three adults were seen feeding and defending the nest; all were banded and thus excluded the fourth bird which I was never able to capture.

During a 1 hour period (1300–1400 EST) on 20 June I recorded 82 feedings by the three adults, 35 by the dull female and the remainder by the other two adults. Most feedings consisted of leafhoppers (Cercopidae: Homoptera). On 20 June I banded and measured the 11 young. Two of the three smallest young were missing (and presumably had died and been removed) on a visit on 27 June. All nine of these young fledged before my next visit on 6 July, when the nest was found with 2–3 cm of excrement atop the grasses.

The presence of four birds around the nest early in the nesting cycle suggests that this nesting was initiated by two pairs of adults occupying the same site; polygyny, therefore, appears unlikely. Of approximately 180 nests of the Tree Swallow I have examined, only one other contained an unusually large number of eggs (also 11). That one was destroyed by a predator before I could determine the number and sex of adults in attendance.—Benedict C. Pinkowski, *60510 Campground, Washington, MI 48094.* *Accepted 27 Aug. 1974.*

Some unusual nest sites of the House Sparrow.—The sites of 28 nests of House Sparrows (*Passer domesticus*) occupying barns and sheds on a farm in western Illinois were recorded during April and May, 1973. Half of the nests were in typical sites, such as under the eaves of buildings, but the other half were in more unusual sites. Twelve were in holes in the once-baled hay in a barn loft. The hay in the barn had been undisturbed for at least 5 years. Entrances to the nest cavities were spaces between boards in the floor of the loft (the ceiling of the main floor), so that the birds had to fly upward to enter. From there a narrow opening extended from 5 to 20 cm horizontally into the hay until it opened into a 10 cm diameter nest chamber. The chambers were lined with feathers and dry grass other than the original hay, but the added material was scanty in comparison with normal nests. The digging of the nest holes in the hay may have been done by rats (*Rattus norvegicus*) or by the sparrows. Sparrows have been reported excavating a nest hole in a rotting tree branch (Philipson, Br. Birds 32:17, 1938). No previous reference to House Sparrows nesting in hay bales has been found.

House Sparrows had also modified and occupied a nest of a Barn Swallow (*Hirundo rustica*) and a nest of an American Robin (*Turdus migratorius*). Similar instances have been previously noted (Bent, U.S. Natl. Mus. Bull. 211, 1958). The Barn Swallow nest we observed was on a joist and was at least a year old and unoccupied when the House Sparrows began modifying it. Large amounts of grasses, feathers, and other materials were added inside and outside until the original diameter was trebled. A dome was constructed over the top, leaving a small entrance at one side.

The robin nest was on a purlin about 20 cm beneath the roof of the barn. Robins had been incubating for 6 days. On the 7th day, grasses and one House Sparrow egg had been added to the robin nest; we never saw the robins at that nest after the first sparrow egg appeared. An additional House Sparrow egg was laid in the nest on each of the next four days, after which the nest was deserted. No dome was constructed over the nest and no lining materials were added to the inside. The sparrows may have been attracted to the open nest due to the roof boards forming a ceiling about 13 cm above the nest rim.—Erica Werler and Edwin C. Franks, *Dept. of Biological Sciences, Western Illinois Univ., Macomb, IL 61455.* *Accepted 23 Sept. 1974.*

Soaring vultures use a dust devil to gain altitude.—An observation during the afternoon of Sunday, 18 July 1965 suggests that large birds are aided by visual perception of thermal air columns. I was driving north of Oklahoma City in a search for dust devils as objects of motion picture photography. The whirls are clearly visible when

dust is lifted to considerable altitudes by the associated rising current of relatively warm air (Sinclair, J. Atmos. Sci., 30:1599–1619, 1973). There were scattered cumulus clouds with bases at about 2500 m; the temperature near the ground was about 38°C; wind from the south was blowing 5 to 10 m sec (meterological data correspond to the record of the U.S. National Weather Service at Oklahoma City).

Near Hennessey at about 14:00 I saw a large dust devil about 0.8 km to the east in a field. I sped north to pass it; then to intercept it I turned east and stopped as the whirlwind approached. It had become invisible after entering a woodlot where dust previously marking the column was less available. Suddenly, about 150 m away, the whirlwind appeared again, well marked by dust lifted from plowed land bordering the woodlot. Almost at the same moment as my renewed sighting, about six vultures, probably *Cathartes aura*, appeared above the woodlot and flew with rapid strong flapping of wings directly toward and into the whirlwind. They gained altitude rapidly; I guessed they were about 150 m high as they passed nearly overhead. Their position related to the whirlwind at the surface showed that the axis of the whirlwind sloped about 20° from the vertical toward the direction of its horizontal motion. While spiraling in the thermal column and drifting northward at a forward speed of about 10 m sec, the birds passed rapidly out of sight as they continued to rise together.

It seems likely that soaring birds use both tactile and visual sensing as well as random flight to locate regions of rising air. Thus both Hankin (Animal Flight, Iliffe & Sons Ltd. London, 1913) and Cone (Am. Sci. 50:180–209, 1962) refer to the start of circling by a flock of vultures or condors initially on the ground, coincident with a gust of wind. Hankin seems to imply visual sensing where he states that Cheels (*Milvus govinda*) often amuse themselves by gliding in and out of dust devils at Rajputana, where sometimes half a dozen, like a row of factory chimneys, are visible at once. Pennycuick (Sci. Am. 229(5):102–109) states that vultures and eagles appear to use visible signs as a glider pilot does. Cone suggests, however, that birds find thermal shells (bubbles) by accident, or by sensing air temperature gradients associated with the buoyancy structure of their thermal core and body, or by monitoring aerodynamic forces.

In the present case it remains inconclusive whether the primary stimulus to avian flight was tactile or visual or both. My perception of events suggests, however, that the vultures rose from the ground because they saw a dusty column and recognized it as the strong updraft they required for low-energy ascent to a great altitude.—Edwin Kessler, *National Severe Storms Laboratory NOAA, 1313 Halley Circle, Norman, OK 73069.* *Accepted 23 Sept. 1974.*

Blue Geese wintering with Sandhill Cranes.—Between 14 January and 26 February 1974 two immature Blue Geese (*Chen caerulescens*) were seen on 14 occasions with a wintering sub-flock of approximately 200 Greater Sandhill Cranes (*Grus canadensis tabida*) on Paynes Prairie, Alachua Co., Florida. Times of observations varied from dawn to dusk. The geese flew to and from roosting sites and fed with the cranes and were usually associated with a group of five cranes. The geese were never seen individually and as far as could be determined, did not leave the company of the cranes. On 19 February the geese and 33 cranes were captured with oral tranquilizers, banded and released (William and Phillips, J. Wildl. Manage. 37:94–97, 1973). When observed one week later, 26 February, the geese were still with the flock. This association is particularly interesting since Harvey et al. (Wilson Bull. 80:421–425, 1968) described Sandhill Cranes as a predator of eggs and young Blue Geese. The fact that the geese were

outside their normal wintering range may have prompted this association.—Stephen A. Nesbitt, *Florida Game and Fresh Water Fish Commission, Wildlife Research Office, 4005 S. Main, Gainesville, FL 32601. Accepted 26 Aug. 1974.*

Renesting and second broods of wild Mallards.—During 1968–71, nesting Mallard (*Anas platyrhynchos*) hens were captured on nest baskets in prairie marshes of Western Stutsman Co., North Dakota (Doty and Lee, J. Wildl. Manage., In press). Each duck was marked with an identifying nasal saddle (Doty and Greenwood, J. Wildl. Manage., In press). Eight of the marked hens were subsequently observed nesting twice in a breeding season on baskets. Five of the hens renested in the same previously used baskets and three were in different baskets but in the same marshes. The time between termination of the first nests and initiation of egg laying in renests averaged 23 days (9 to 66 days). The long delay for some of the ducks indicates that other nesting attempts could have taken place, but periodic checking of all nest baskets precluded the possibility that interim nesting occurred in them.

Three of the eight renesting hens had hatched clutches of eggs earlier in the season. The successful hatch of the first and second observed clutches of two hens was deduced from the appearance of egg membranes and shells, and the absence of any sign of duckling mortality. These hens laid the first egg of their second clutch approximately 22 and 25 days after termination of the first nests. There were 11 and 10 hatched ducklings in the first broods and 6 and 3 in the second broods. The third hen hatched five of six eggs in its first observed clutch but the ducklings died of exposure soon after they left the nest. A temporary confinement pen set around the nest basket (for capture and marking of young) had apparently prevented the hen from properly brooding the ducklings during a rainstorm in the evening of the day of hatching. That hen laid the first egg of its second clutch in the same basket 11 days after the earlier hatch, but the hen died after laying four eggs in the second clutch. The apparent cause of death was peritonitis possibly brought on by oviduct necrosis due to an impacted, thin-shelled egg.

Instances of individuals renesting after hatching eggs in earlier clutches have been reported for the Wood Duck (*Aix sponsa*) by Barnes (Auk 65:449, 1948), Hester (Proc. S.E. Assoc. Game and Fish Comm. 16:67–70, 1965), Grice and Rogers (Massachusetts Div. Fish and Game, Final Rep., Proj. W-19-R, 1965), McGilvrey (Auk 83:303, 1966), Rogers and Hansen (Bird-Banding 38:234–235, 1967), and L. Fredrickson (pers. comm.); the Black Duck (*Anas rubripes*) by Stotts and Davis (Chesapeake Sci. 1:127–154, 1960), and Benson and Foley (N.Y. Fish Game J. 9:73–92, 1962), the Pintail (*A. acuta*) by Sowls (Stackpole Co., Harrisburg, Pa. and Wildl. Manage. Inst., Washington, D.C., 1955), the Mallard on managed areas (Burger, Proc. N.E. Fish and Wildl. Conf., 1964; Bjarvall, Wilson Bull. 81:94–96, 1969), and released Mallards (Benson and Foley, N.Y. Fish Game J. 9:73–92, 1962).

I thank Charles W. Dane for his review of the manuscript.—Harold A. Doty, *Northern Prairie Wildlife Research Center, U.S. Fish and Wildlife Service, Jamestown, ND 58401. Accepted 8 Aug. 1974.*

Artifactual clutch size in Sooty Terns and Brown Noddies.—Certain seabirds including Procellariiformes and some Laridae usually incubate single-egg clutches, but have been found occasionally with more than one egg. Several investigators have con-

cluded that "two-egg" clutches reported in albatrosses occur only when the eggs are laid by different females (Tickell and Pinder, Ibis 108:126–129, 1966; Fisher, Auk 85:134–136, 1968).

Sooty Terns (*Sterna fuscata*) and Brown Noddies (*Anous stolidus*) sometimes incubate two eggs but usually just one (Watson, Papers Tortugas Lab. Carnegie Inst. Washington 2:187–255, 1908; Murphy, Oceanic Birds of South America, Macmillan, New York, 1936; Shallenberger, Elepaio 30:61–64, 1970; Berger, Hawaiian Birdlife, Univ. Press of Hawaii, Honolulu, 1972). However, there has been no quantitative investigation of the frequency of two-egg clutches in these species, nor have there been attempts to determine if both eggs in two-egg clutches were laid by the same female. In 1971 and 1972 I studied both of these problems in the Sooty Terns and Brown Noddies breeding on Manana Island, Hawaii. Approximately 100,000 Sooty Terns and 30,000 Brown Noddies breed on Manana annually (Brown, MS). The Sooty Tern eggs are laid directly on rock, mud, or sand, whereas Brown Noddy eggs are only laid upon rocky substrate.

In 1971 I hammered a stake into the ground in the Sooty Tern colony before egg-laying began. I attached one end of a graduated wire cord to the stake, and, by also using a compass, was able to record the precise distance and compass bearing from the stake of any egg within the radius of the cord. On 31 March, when the Sooty Terns first laid in the area, and on 1, 4, 9, 13, 16, and 21 April I located and numbered 91 eggs laid within 3.05 m of the stake. I could determine that a "two-egg" clutch was artifactual if at least one of the eggs had been found at a different location and therefore had rolled to the present site. The number of eggs in the plot increased from 77 to 91 between 9 April and 21 April, whereas the number of "two-egg" clutches increased from 4 to 10. Only three of the "two-egg" clutches could possibly have resulted from eggs laid at the same site.

In 1971 I counted all Brown Noddy eggs on Manana during the first week in June, about 3 weeks after laying had begun. Only 179 of 11,932 nest sites, about 1.5%, contained clutches of two eggs. In July 1971 I marked 31 clutches of two eggs and checked them every 3 days. In six instances both eggs hatched (19%); in 17 instances one egg hatched (55%), and in eight instances neither egg hatched (26%). Considering the six cases where both eggs hatched, the eggs of one clutch hatched 12 to 15 days apart; the eggs of two clutches hatched 9 to 12 days apart; the eggs of one clutch hatched 3 to 6 days apart, and the eggs of two clutches hatched on the same day.

At most a few percent of the female Sooty Terns and Brown Noddies on Manana lay clutches of two eggs. However, for both species doubt exists that any females lay two eggs. The high percentage of clutches of two eggs in the Sooty Tern that are known to be artifactual suggests that those clutches for which this information is lacking may be artifactual also. The separation in time of hatching of up to two weeks in the Brown Noddy clutches of two eggs indicates that at least some of these clutches were probably laid by more than one female. Lacking a convincing demonstration that the birds sometimes lay two eggs, it may be best to assume females of these two species lay a single egg.

This paper is based upon a dissertation I submitted to the University of Hawaii in partial fulfillment of the requirements for the Ph.D. in Zoology. I thank Dr. Andrew J. Berger for guidance and criticism during this study. The Hawaii State Division of Fish and Game kindly granted me permission to work on Manana. This study was supported by the Dept. of Zoology, University of Hawaii; an NFS Graduate Fellowship; and a Mount Holyoke College Faculty Grant.—William Y. Brown, *23 Hudson Street, Cambridge, MA 02138.* *Accepted 7 Oct. 1974.*

THE PRESIDENT'S PAGE

A strong interest in wildlife conservation has always characterized the membership of the Wilson Ornithological Society, in response to which we have traditionally maintained a Conservation Committee. As one thumbs through a set of volumes of The Wilson Bulletin, one encounters Conservation Committee reports of varying length, scope, and quality, as well as outright gaps in the record. For many years the Committee endeavored in its report to present a series of conservation news items—a roundup of important losses and gains for wildlife during the previous year. Such multiple coverage meant that the presentation of individual items was necessarily somewhat superficial. On the other hand, some Conservation Committee reports consisted of major analyses of single subjects.

The increase of general interest in environmental matters has led to the publication of several kinds of progress reports on conservation. Most appear more frequently, and can thus bring news items more quickly to readers, than the annual Committee report in The Wilson Bulletin. For the past several years the Council of the Wilson Society has given its approval to the concept of a project-oriented Conservation Committee, with the mission of presenting to the W.O.S. membership detailed and informed studies of individual current issues in wildlife conservation. Whenever possible, the Committee's reports are to present objective analyses of varying points of view, indicating the data (if any) that support each. If the Committee sees fit, it can formulate specific recommendations and forward these to the Resolutions Committee, to be considered by the W.O.S. membership at the next annual meeting.

In 1973 I appointed Dr. Clait E. Braun of the Colorado Division of Wildlife as Chairman of the Conservation Committee, on the enthusiastic recommendation of Dr. Gustav A. Swanson, the retiring Chairman. I asked Dr. Braun to assemble two subcommittees of knowledgeable specialists, to investigate and report on the present status of eagles and of Sandhill Cranes, both groups being the subject of no little controversy in the western states and provinces. The first subcommittee report appears in this issue of The Wilson Bulletin, and the second will appear in June. These reports were presented to the Council at the 1974 meeting, and were accepted with hearty commendations to Dr. Braun and his Committee members. I believe that readers of the Bulletin will be impressed, as was the Council, with the thoroughness and the objectivity of these reports.

In 1974–1975, a new Committee under Dr. Braun's chairmanship has been examining the effects of alteration of sage brush on the native avifauna of this habitat, as (to use Dr. Braun's words) "projects designed to 'reclaim' the land from sage brush have been in vogue in recent years." The report of this study will be presented to the Council at the Bozeman meeting in June, and will subsequently be published in The Wilson Bulletin.

These achievements of the Conservation Committee, praiseworthy though they may be, satisfy neither Clait Braun nor me. The Committee exists not only to report to you, but also to *listen* to you. We urge members of the W.O.S. to participate in the activities of the Committee by suggesting possible issues for investigation; by volunteering specialized knowledge to assist the Committee in its research and its evaluations; indeed, by volunteering to *serve* on future Committees; and even, if you wish, by registering your disagreement with the conclusions presented in the Committee's reports. Address your communications to: Dr. Clait E. Braun, Wildlife Research Center, P.O. Box 2287, Fort Collins, Colorado 80522. The questionnaires returned by Wilson Society members some years ago indicated that many of you thought the Society should take a more active part in conservation activities. The Conservation Committee exists as a medium whereby members can express their personal concerns, and we hope you will thus use it.—Kenneth C. Parkes.

EDITORIAL

We have made some changes in The Wilson Bulletin beginning with this issue—a dues increase is not one of them. Inflation is seriously affecting scientific publications (see Abelson, Science 186:693, 1974), but rather than raise dues now we have opted to make changes that will reduce publication costs and make maximum use of page space without reducing the quality or number of papers published, the clarity of writing, or the aesthetic appearance of our journal. The changes have been made after long deliberation and consultation with Allen Press, members of the Wilson Council, and others. Most noticeable, page size has been reduced slightly at the recommendation of Allen Press. The amount of printing on a page has not been reduced, thus effectively we have reduced margins and also saved paper and postage. Our cost savings for this change will be substantial. Second, I have made numerous style changes to save space. These include greater use of standard abbreviations for all measurement units, the use of % instead of percent, greater use of numerals to replace spelled out numbers, deletion of some commas in literature citations, and elimination of repetition of author's names in the literature cited. (See also *Suggestions to Authors* printed elsewhere in this issue.)

This space-saving will in some cases save the society money. It will frequently save page space that can be used for news, announcements, reviews, or additional general notes. Other changes, such as a change in grade of paper, reduction of type size in major articles, not starting major articles at the top of a new page, and a change in method of printing, have been discussed but considered of no economic benefit or aesthetically objectionable. We could at the moment save about $25 per issue by mailing the Bulletin in plastic envelopes. Since plastic is a petroleum product this advantage is not likely to last, and since we are a conservation organization it seems more appropriate that we continue with paper envelopes.

I am particularly grateful to Kenneth Parkes, George Hall, John Hubbard, and Arly Allen for their careful study and advice with regard to these changes. The final decision on style changes was mine, however, and I accept responsibility for it. I will be grateful for any comments regarding these changes, for after all, this is your journal and I am anxious to serve and satisfy the ornithological community that is the Wilson Ornithological Society.

As a recent past-treasurer of the Wilson Society I would like to suggest some additional ways we can minimize our operating costs. Please pay your dues as promptly as possible. By doing so you save the society the expense of sending a second notice. Furthermore, our treasurer keeps only what is necessary to pay operating expenses in a checking account and the balance of our general funds is kept in savings accounts and earns interest. Thus, by paying dues promptly the society realizes an additional financial benefit. Failure of a member to promptly notify the treasurer of an address change not only results in the member getting his Bulletin late, but also costs the society additional postage if the journal is returned to Allen Press. Please notify the treasurer of your address change as soon as possible and help us reduce these expenses. Finally, I encourage you to consider voluntary contributions to the society to support publication of our journal, the continuation of our various awards, and the maintenance of the Josselyn Van Tyne Library.

ORNITHOLOGICAL NEWS

1975 ANNUAL MEETING TO BE HELD JOINTLY WITH THE COOPER ORNITHOLOGICAL SOCIETY

The Wilson Ornithological Society will hold its 56th Annual Meeting jointly with the Cooper Ornithological Society on the Montana State University campus in Bozeman, Montana, from Wednesday to Sunday, 11–15 June 1975. Co-hosts will be the Sacajawea Audubon Society and Montana State University. This is Montana's Land Grant School with an enrollment of about 8,000 students. Bozeman has a population of about 20,000 and is located in the fertile Gallatin Valley of the east slope of the Rocky Mountains. It is about 300 miles from Glacier Park, 90 miles from Yellowstone Park, 60 miles from Chet Huntley's dream-The Big Sky of Montana, and 20 miles from the Bridger Ski Bowl.

Detailed information about accommodations, transportation, field trips, and the host area has been sent to members with the advance registration forms and call for papers.

Dr. Douglas James, Division of Biomedical and Environmental Research, Energy Research and Development Administration, Washington, D.C., 20545, is Chairman of the scientific program, which will feature a symposium on birds and their habitats, and Dr. Clifford V. Davis, Department of Biology, Montana State University, Bozeman, Montana 59715 is Chairman of the committee on arrangements.

SYMPOSIUM ON AVIAN HABITATS

The Wilson Ornithological Society and the Cooper Ornithological Society will co-host this symposium at their joint meeting at Bozeman, Montana, on 11–15 June 1975. The symposium is organized by Douglas James and will focus on birds and the vegetational environments that they occupy. John Emlen will introduce the symposium, and James Karr will present a closing summary of the papers. Speakers have already been invited, and many have already accepted and presented their titles for their papers. There will be a wide variety of subjects treated, ranging geographically from the Americas to Africa and ecologically from the tropics to tundra.

NECROLOGY

We regret to report that C. Chandler Ross, Treasurer of the Society from 1963–1968 and an Elective Member of the Council from 1968–1971, died on September 22, 1974 as a result of injuries sustained in an accident. Mr. Ross has bequeathed his natural history library to the Wilson Ornithological Society's Josselyn Van Tyne Memorial Library.

ORNITHOLOGICAL LITERATURE

Breeding Biology of Birds. Proceedings of a Symposium on Breeding Behavior and Reproductive Physiology in Birds. Edited by D. S. Farner. National Academy of Sciences, Washington, D.C., 1973: 515 pp., illustrated with drawings, charts, maps, photos; paperbound. $15.50.—This gem reviews broadly many of the most active areas of research in birds. The symposium presentations and discussions are the result of an attempt at ecumenicism in bringing together wildlife biologists, ornithologists, and comparative endocrinologists, to discuss the state of their sciences in early 1972.

D. S. Farner's introduction provides a concise outline of his scheme of the environmental and physiological control of reproduction in birds. Two later chapters detail the recent advances in the field of neuroendocrinology and the hypothalamo-hypophyseal physiological control system of birds. I. Assenmacher traces the physiology of gonadotropin and prolactin. He discusses the current evidence of the existence of two distinct gonadotropins in birds, and he reviews the evidence "that an antigonadal effect of prolactin in birds, whether migratory or not, can no longer be accepted as a general concept," in contrast to mammals. B. K. Follett's chapter on the neuroendocrine regulation of gonadotropin secretion in avian reproduction is neuroanatomical in emphasis and includes a review of histochemical work on catecholamines and the neurosecretory tracts involved in hypophyseal control. He also discusses the perception of light and daylength. A. Oksche contributes to the discussion of neuroanatomy, and Farner points out the progress being made in linking the neuroanatomical and physiological studies of birds. I found the informal discussions following these chapters to be full of previously unpublished, uncompleted results of research contributed by activists in these fields.

In two chapters on more gut-oriented physiology, M. D. Scott discusses the importance of nutrition in reproduction and shows the results of studies on captive birds in determining dietary requirements for maintenance and reproduction in domestic and game birds. The discussants particularly R. K. Murton and A. Watson, point out how little is known of nutritional problems of birds in the wild. J. R. King summarizes the available data on the caloric cost of reproduction in his chapter, and he suggests the idea that incubation may not "cost" a bird anything because it may simply use its normal metabolic heat to warm the eggs (calorie-wise, the normal heat loss is more than adequate to account for the heat needed for embryonic development). In a following discussion S. C. Kendeigh expresses disbelief in the "no-cost" hypothesis, but his argument assumes that a bird cannot adjust its proportions of heat loss through the skin, brood patch, and respiration as conditions may indicate. King notes that energy costs of breeding appear to be more intensive for females than for males, at least in terms of gonadal development, but nothing is known about the energetic cost of male breeding behavior. The data that King uses for discussion of "cost" are strictly physiological or nearly so, and it would be of interest to determine "cost" also in terms of the long-term effect of breeding on survival and future reproduction of the adult birds.

The chapters on ecology and behavior vary considerably in their comprehensiveness. F. McKinney discusses the "ethological aspects of reproduction" in species that he has studied, and he relates the displays of two eiders and two ducks to a difference in their feeding behavior, assuming that the sociality and conspicuousness of displays and the permanence of the pair bond in birds are ultimately caused by the different feeding behavior of the species. McKinney's descriptions suggest that species differences in behavior may be selected more directly by predators than food in the eiders. G. Orians

relates his models of selection for mating systems in birds to R. Levins' fitness-set models by suggesting that the patchiness or grain of different habitats is a major selective component for the evolution of social systems. In discussing the natural history of incubation, R. Drent reviews the problems of heating and cooling of the egg, the physical and gas-exchange problems of incubation, the synchronizing of hatching, and how the parent continually readjusts its behavior to the condition of the eggs. He also discusses the anti-predator behavior of birds at the nest. Drent suggests several field and lab problems for further study. C. G. Beer gives an intriguing discussion of the limits of usefulness of a reductionist physiological approach to the study of behavior, while at the same time he emphasizes the important contributions to an understanding of the whole of behavior by picking apart its parts—the Canary work at Cambridge and the Ring Dove work at Rutgers, with all the complex interplay between environmental factors, hormonal feedback systems, and the previous experience of the bird. Beer also discusses his studies of individual recognition by voice in breeding gulls. D. A. Jenni's brief discussion of mating systems in birds unfortunately pre-dates the spirit of his more successful recent (Am. Zool., 1974) paper where natural selection producing "strategies" of social behavior, not physiological means, are given as explanations for evolution. The informal discussion following this behavior section gives a revealing look at reductionism as a philosophical means to provide explanations to biological questions in comments of Farner and Beer.

R. E. Ricklefs's long chapter (71 pages) on "fecundity, mortality, and avian demography" is at once a lucid review of principles of population ecology and a discussion of the reproductive "strategies" of birds. I noted some errors here. Morel's work with *Lagonosticta senegala* is said to have reported that yearly survivorship increases with age—her data in fact do not show this nor did she she say this happened. Ricklefs shows us how to derive a life table, and he uses available life table data for birds to compare the ecology and evolution of breeding effort in the same straightforward style that characterizes the similar discussion in his recent text *Ecology* (Chiron Press, 1973). One can see that Lack, the guiding light of the last three decades in interpreting life history phenomena in terms of natural selection, is gone, for on p. 428 Ricklefs leaves us with the query, "But if adult mortality was [sic] to decrease and a population became stabilized at a higher density, would not intraspecific competition reduce food availability and, hence, clutch size?" This last appears to this reviewer to suggest confusion between the idea of a selected adaptability of an individual to adjust its reproductive effort to local conditions, and the idea (that Lack questioned) of selection for lowered reproductive effort in individuals regardless of the high effort of their neighbors. Ricklefs does not attempt to explain how it might happen that an individual that leaves fewer offspring than his neighbor would be favored by natural selection within the population.

K. Immelmann discusses the role of the environment in reproduction in a review like his more extensive review in *Avian Biology*, vol. 1. He emphasizes, as does Farner, the high degree of predictability of photoperiodic changes as the reason why most birds cue in on daylength to time their breeding. He overlooks my experimental evidence (Univ. Calif. Publ. Zool. 90, 1969) that rainfall and local insect abundance is sufficient in some birds of arid habitats to bring about gonadal development and breeding. H. J. Frith adds to the field evidence that the breeding times of some waterfowl are direct responses to rains.

L. von Haartman's "changes in the breeding bird fauna of north Europe" summarizes the well-documented shifts in range and numbers of *Vanellus vanellus*, *Turdus merula*,

Erithacus luscinia, *Carpodacus erythrinus*, and several other species. The increases were often synchronized among several species. It is not certain whether long-term weather changes, forest succession, or land use are mainly responsible for these changes. J. W. Aldrich considers the problem of sex ratios of adult waterfowl and possible implications for management. T. S. Baskett presents a comprehensive view of how the more academic interests and results of most of the symposium people are related to the practical interests in the management of wildlife.

The book has several highly worthwhile chapters and is an exciting addition to the field. It should be read by avian biologists, and some of its chapters may be good supplementary reading for a course in ornithology as a biological science. Sure it's expensive for a paperback, but it's a lot cheaper than *Avian Biology*.—Robert B. Payne.

The Natural History of French Frigate Shoals, Northwestern Hawaiian Islands. By A. Binion Amerson, Jr. Atoll Research Bull. 150. Smithsonian Institution, Washington, D.C., 1971: xv + 383 pp., 74 figures, 149 tables. No price given.—French Frigate Shoals (FFS) is a crescent-shaped coral reef enclosing 12 low sandy islands and two pinnacles, the latter being the last projecting remnants of the volcanic mountain upon which the reef system rests. Amerson gives primary emphasis to the vertebrates and vascular plants, but they are introduced with a thorough discussion (62 pages) of the geology, climate, and history of the shoals, including accounts of all known visits by ships. Detailed descriptions of the past and present appearance of each island are included. The transformations of East and Tern Islands by the military before, during, and after World War II are clearly described and photographically documented. When we read that Tern Island's dimensions (450 × 1800 ft) were augmented by 660,000 yds^3 of dredged coral in 1942, we watch its subsequent changes by comparing early maps and a series of photographs showing the new island (350 × 3100 ft) gradually clothed in exotic (30 species) and native (7 species) plants. These accounts provide an excellent background for understanding the variations in species composition between the islands.

The main body of the monograph is based upon 10 survey trips (203 days) to the atoll by members of the Smithsonian's Pacific Ocean Biological Survey Program (POBSP) from June 1963 to June 1969, supplemented by a wealth of other published and unpublished data. One feels from the sheer mass of information that no data exist anywhere about FFS that haven't been found and included.

Forty-four species of vascular plants are known from the atoll; 30 are introduced, primarily to the two most disturbed islands (Tern and East). The flora of each island is treated separately, with comments on past and present distribution, including introduction attempts, for all species known to have occurred. There are many points of interest: for example, between 1965 and 1969 the southeastern sandy crest of Trig Island was invaded by *Tournefortia* bushes, which developed a stand 5 feet tall; as a result, the breeding population of Red-footed Boobies increased eightfold! What does this tell us about factors regulating the population of some breeding sea birds?

All vertebrates (except fish) known from the atoll (2 reptiles, 44 birds, 7 mammals) are discussed in detail. Reptiles are represented by the largest population of green sea turtles in the Hawaiian Islands, and an introduced gecko (on Tern and East Islands). Amazingly, no rodents have become established. Pigs were released and died out in the 19th century. Dogs and cats accompanied military occupation, but only dogs remain, pets of the U.S. Coast Guard on Tern Island. The last cat died on Tern Island

in June 1966, and Bulwer's Petrels began nesting later that year, increasing to 10 birds by 1969. Large numbers of Hawaiian monk seals were discovered in 1859, and their exploitation began that year. They were observed in 1886, but went unreported thereafter until 1950, when one was seen. The population is growing, with 171 animals estimated for the atoll in 1967. Man continues to influence the area: inhabited Tern Island has only half the number of breeding sea bird species as comparable Whale-Skate Island, which was never occupied. East Island, abandoned by man in 1952, supports an intermediate but growing number. It is heartening to note that populations of many species are increasing with the rigid protection being given to this and surrounding islands in the Leeward chain.

The avifauna consists of 18 resident seabirds, 5 migrant shorebirds, and 21 species of infrequent or accidental occurrence. These are introduced in a broad section discussing the breeding cycles and population fluctuations of the residents and migrants, and the status of the others. All species then receive treatment from two perspectives; detailed accounts of the avifauna of each island are followed by equally detailed accounts of each species, including lists of all records for each island upon which they occur. This procedure is both useful and repetitive, for most information is presented or discussed three times. There is far more of interest in this mine of information than can be discussed here; a few samples will suffice to show the diversity of available information. Interisland movement of resident species occurs regularly. Of 8,238 banded birds recaptured on FFS, 269 (3.3%) originated on other atolls, and of 67,027 birds banded at FFS, 246 (0.37%) were recaptured elsewhere, primarily on other islands in the Hawaiian Leewards, or on Johnston Atoll (half the records). Eight Ruddy Turnstones banded on St. George Island, Alaska, were recaptured on FFS, one having made the 2,272 mile flight (Amerson incorrectly gives distance as 1,800 miles—see Thompson, Living Bird 12:5–24, 1974) in less than 4 days, one of the fastest migratory flights ever documented (649 miles/day minimum). The colony of 150 pairs of blue-faced boobies disappeared from East Island during military occupation, although birds occasionally roosted there. Following the island's abandonment, the number of roosting birds increased, but breeding did not begin again until 1966, 14 years after men had left. The nesting population has thereafter steadily increased. Throughout the accounts is a *basso continuo* of human-bird interactions, and one wishes this could have been brought together in one section, a task now facing the readers.

This work is a foundation piece that has cemented together an enormous mass of information from incredibly diverse sources. Some readers will certainly dispute the necessity of including all the data, but everything is available for those who want it, from La Perouse's nearly fatal discovery of the shoals in 1786 to the last POBSB sight record in 1969. Anyone interested in the Hawaiian Leewards, FFS, or sea bird distribution owes Amerson a debt of gratitude for the effort involved in pulling this information together. It will be indispensible for future work in the area. However, most readers will regret that almost no attempt has been made to broaden the perspective to include information from other atolls, especially those nearby. This work is simply unconnected to other regional works. Are sea bird populations different elsewhere in the Leewards? Is anything unique to FFS? Are the breeding cycles representative of those on Kure and Midway, in cooler waters to the north? Published information and POBSP data was available when this monograph was in preparation. It should also be noted that this is primarily a distributional work, as would be expected from the original research effort (infrequent trips to the atoll over a 7-year period). Little is presented about the breeding biology of the resident populations, and almost none

of the major papers on the ecology or behavior of the resident sea bird species are cited. In this sense it is a foundation, strong and substantial in its own right, yet awaiting a more detailed and elaborate structure to be built upon it.—Cameron B. Kepler.

The Behavioral Patterns of the Eastern Bluebird (*Sialia sialis*). By David C. Krieg. Bulletin Number 415. New York State Museum and Science Service. Albany, New York. 1971: v + 139 pp.—In this small book the author describes the species-typical behavior of the Eastern Bluebird. Because of the appeal of this species to laymen and to ornithologists alike, it is surprising that a description of behavior is so long in coming. The book seems to be intended primarily for the ethologist, but it can be read with interest by others as well.

The author observed wild bluebirds in western New York through five breeding seasons, and several captive pairs for two years. He also observed the birds on their wintering ground in Florida.

He has described their behavior in five main sections: Maintenance Activities, Agonistic Behavior, Territory, Pair Formation, and Courtship. In each of these Krieg describes the behavior of the Eastern Bluebird and compares it to that of other passerines, and especially of other thrushes. Maintenance and agonistic behavior are quite similar to that of other species studied, but differ in small details. Pair formation and courtship behavior likewise in many respects resemble the behavior of other passerines. Krieg here makes little reference to the admittedly rather limited literature on courtship and reproductive behavior of other thrushes.

An interesting conclusion that should be taken into account by the many boy scout and other groups that build and set up bluebird houses in hopes of increasing the local bluebird population is that increasing the number of boxes does not necessarily increase the population of bluebirds. It is not so much the number of boxes as the selective placement of boxes throughout suitable habitat that brings about an increase in the number of breeding pairs in an area. Each pair defends a territory ranging in size from 5.1 to 28.7 acres (average for two years 13.6 acres), and may include several nest boxes within the territory. It is in fact desirable that several boxes be available within each territory in case of failure of one nest. A pair will seldom renest in the same box if the nest has failed for any reason. If no other nest site is available within the territory the birds will usually leave.

One of the book's strong points is its extensive coverage of the behavior of this popular North American bird. The very good to excellent outline drawings by Anthony Moriello are a definite bonus in conveying an understanding of the various postures involved. The comparison of the bluebird's behavior to that of other thrushes is a laudable attempt, but falls short of what it might have been because of the use of so few references. Almost all the references to other thrushes are to Dilger's work on *Catharus* and *Hylocichla* (Auk 73:313–353, 1956).

After completing the book there lingered a question in my mind about the audience for which the book was actually intended. If scientific, the descriptions of behavior often fall short of the completeness that an ethologist might desire. There is disappointingly little reference to current ethological theory. Likewise, the comparisons with other species are not extensive enough, especially in territorial and courtship behavior, to allow the reader to put bluebird behavior into proper perspective. If the book is intended mainly for general readers, there are too many undefined technical terms for the text to be entirely comprehensible. I suspect, for example, that very few laymen and not

many biologists carry in their heads the definition of the word "gamosematic" which Krieg uses but does not define. I was not able to find a definition of it in any of the books in my personal library. In other places the author depends for his definitions on references that may be difficult for the average reader to obtain. A sentence or two could have clarified the term and made the book much stronger.

Some of the terms used in describing behavior seem unfortunate. One that annoyed me especially was "Prenest Building." I assume that this refers to behavior of the pair subsequent to pair formation, but prior to nest building. A better term would have been "pre-nestbuilding," or something of the sort. This criticism perhaps should be levelled at the editor as well as the author. For a state technical publication the text contains an inordinate number of spelling and grammatical errors, again a criticism to be shared by both the author and the editor.

I found the organization of the book confusing in places. Descriptions of vocalizations are scattered throughout. Several times when references to different vocalizations appeared I had to thumb back through the book to see if I had missed an earler description of them. In a couple of cases I never did find an adequate description.

Although it is disappointing in many respects, Krieg's work does represent the most extensive description of hluebird behavior published to date, and by and large is a competent work. My criticisms result from the book's falling short of its potential. Many readers will, nevertheless, find it very interesting and informative.—William L. Thompson.

Cranes of the World. By Lawrence Walkinshaw. Winchester Press. 1973: 370 pp., 4 col. pls. $25.00—Not since 1897 has a book been published concerning all species of cranes. Walkinshaw presents an extensive literature review and many personal observations in his long awaited volume. There is a chapter for each species, and the length of each chapter reflects the amount of study the species have received.

A short introduction discusses distribution, nesting season relative to latitude, characteristics, classification of extant species, voice, and conservation measures. I found the list of recorded fossils especially useful.

More than 21 pages are devoted to the distribution of the two subspecies of the European Crane. Much information on spring behavior, clutch size, nesting and incubation behavior is also presented. Less is said about diet, feeding behavior, egg laying, and nesting biotopes. The sections on copulation, voice, and molt belong in the introduction because they cover several species other than the European Crane.

The length of the chapter on the Black-necked Crane (7 pages) reflects the dearth of information available on the species. Walkinshaw devotes four pages to distribution and covers everything else in three pages.

The Hooded Crane chapter has no introduction and states that the breeding biology is little known, and breeding range and young are unknown. Most of the chapter concerns distribution.

The chapter on Sandhill Cranes is the longest in the book and considers all six subspecies, but especially life history data for the lesser and greater subspecies. In contrast, the account of the Cuban Sandhill Crane is brief because of lack of study in recent years. The Canadian subspecies is also dealt with briefly. Persons interested in the Lesser and Greater subspecies should be delighted with the chapter. However, portions of the account are confnsing. While discussing Lesser Sandhill Cranes (p.

92) the author discusses the distribution of Greater Sandhill Cranes, and under Florida Sandhill Cranes (p. 131) movements of color-marked Greaters are included. On page 91 a list of counties where Sandhill Cranes have been found (other than West Texas) includes Bailey County. This county is the principal wintering area for Lessers and is situated on the border of New Mexico and should not have been listed.

The Japanese Crane chapter is adequate, but the discussion of winter behavior under distribution is confusing and deserves separate treatment. Although the nest, eggs, young, voice, and food are well handled, the sections on territory and dancing ought to be in the introduction because all species are discussed.

Whooping Cranes are discussed adequately in 22 pages, including recent information published since Allen's monograph (Nat. Aud. Soc. Res. Rept. No. 3, 1952).

Because the White-naped Crane nests in Siberia much of the chapter is based on the literature. Walkinshaw personally observed them on wintering grounds and studied the nesting activity of captives.

Both subspecies of the Sarus Crane are discussed. More detail on the nesting cycle is provided than in other chapters reflecting Walkinshaw's personal interest and experience with the species.

The Brolga or Australian Crane chapter is one of the most interesting with Walkinshaw's personal observations enlivening the account. The description of the young is too brief, but other topics are adequately discussed.

The Siberian White Crane nests in Siberia and is discussed largely from the literature. Winter behavior, being well known, is emphasized and little is presented on breeding. The section on distribution, usually following the introductory remarks, is for some reason at the end.

The Wattled Crane is adequately covered as are other African cranes. Considerable detail is presented on breeding, eggs, young, voice, and distribution.

The Demoiselle Crane chapter is short but adequate. Literature accounts provide most of the life history.

All topics are adequately discussed concerning the Stanley Crane and a unique section is devoted to behavior toward other birds and mammals. This section is interesting and would have been welcome in other chapters. The young are discussed in more detail than usual.

Both subspecies of the West African Crowned Crane are discussed, but more information is presented on the West African subspecies than the Sudan form. Considerable information is presented on the South African Crowned Crane, and Walkinshaw's personal observations of both species add immensely to the text. The second paragraph differentiating between *Balearica* and other crane genera in Chapter 15 would have been more appropriately included in Chapter 14.

The bibliography contains numerous references. However, it is confusing and each reference should have been listed alphabetically and not under each species.

Many of the photographs are blurred and indistinct. The photographs of the Brolgas on pages 3 and 227 are nearly identical. Other photos should have been centered (e.g. page 232). The photograph of the Hooded Cranes (page 68) is in the wrong chapter and the photo of the hybrid young (page 73) belongs on page 59 with the discussion. On page 89 the caption reading "Canadian Sandhill Crane with young" must refer to a yearling since both appear in adult plumage. Unfortunately, there is not a color photograph for every species; however, ten are represented.

The 22 tables should have been included in species accounts rather than being lumped together in the back. Several occupy only half a page.

Persons who are not authorities on world geography will have difficulty with species ranges. Range maps would have been an improvement. Apparently this was the publisher's decision, because Walkinshaw (page 44, paragraph 4) refers to a map that does not appear, and he later published range maps for all species and subspecies. These maps may be obtained directly from the author.

A few typographical errors were found, and an index is not provided.

Although there are some minor problems with the book, Walkinshaw has amassed an enormous amount of information. The book should serve professional ornithologist and layman alike. Anyone purchasing books for their colored plates should avoid this one.—Carroll D. Littlefield.

A Guide to the Birds of Trinidad and Tobago. By Richard ffrench. Livingston Publishing Co., Wynnewood, Pa., 1973: 512 pp., 28 col. pls. and 41 text figs. by John O'Neill, 8 full-page portraits by Don R. Eckelberry. $12.50.—This is a most welcome addition to the literature on the Neotropics. More of a handbook than a traditional field guide, it provides an up to date summary of the information available on the birds of Trinidad and Tobago. The species accounts include information on habitat and status, range and subspecies, banding status, description, measurements, voice, food, nesting, behavior, and occasional general notes. The accounts are short for rare or poorly known species, but a full summary of the life history and behavior is presented for the several species for which extensive information is available. For the most part this is a result of the recent detailed studies of Trinidad and Tobago birds conducted by R. ffrench, D. Snow, B. Snow, A. Lill and others. Life history information from other parts of the species' range is often presented for contrast or to flesh out accounts of species poorly studied in Trinidad and Tobago. In each case the source of information is clearly indicated. These species accounts are well done and make interesting reading.

The inclusion of banding and recovery data and body weights is nearly unique for books of this sort. The weight data will be particularly welcome to those interested in the ecology, physiology, and growth of neotropical birds. Species considered by ffrench to be of dubious occurrence in Trinidad or Tobago, or ones that might be expected to occur but are now represented only by inadequate sight records are included in the text in the regular taxonomic sequence with the accounts set off by brackets. This procedure obviates the need for a separate hypothetical list, and facilitates consideration of all possibilities when one is trying to identify an unusual or unfamiliar species in the field.

In addition to the species accounts, 35 pages are devoted to a rather thorough introduction including discussions of the history of ornithology and conservation in the islands, the climate, environments, and habitats (supplemented by well-chosen photographs) and an over all view of the ecology, distribution, breeding seasons, and migration of the birds. This section is well done, interesting, and should be required reading for any ornithologist or birdwatcher visiting these islands. Maps of Trinidad and Tobago showing major features and locations are included on both flyleafs. Had they been separated, one to each flyleaf, and reproduced much larger their usefulness would have been greatly improved.

No book is without faults, although this one has perhaps fewer than its share. A few comments or suggestions can be made, although at least some are simply personal preferences. Perhaps resulting from an over-reaction to the approach of a previous book (*The Birds of Trinidad and Tobago*, Herklots, G. A. C., 1961, London, Collins), which

gave an overly detailed feather-by-feather description of each species, the section on description in the species accounts seems at times too abbreviated and does not always call attention to characters separating similar species. However, at times this has been done most successfully. Only after this book has been used in the field can this point be fully evaluated.

The plates and text figures by John O'Neill are a decided improvement over those previously available, and the portraits by Don Eckelberry are superb. Even so, some questions arise. Because it was not possible to illustrate every species I fail to see why the male Black-tailed Tityra and Yellow-legged Thrush were illustrated by text figures (38 and 41) when both were portrait subjects and the different-appearing Tobago race of the latter was also shown in Plate XXI. The space might have been better used for figures of species not otherwise illustrated. Similarly, at least 10 species included in the color plates are "rare visitors" or "possible rare resident" and in the case of *Amazilia fimbriata*, one now believed to have been mistakenly included in the avifauna. These could have been either omitted (the Small-billed Elainea) or presented just as effectively as a text figure (the King Vulture, Scaled Ant Pitta, and others). The space saved, amounting to at least one full color plate, could have been used to portray some of the commoner species that were not illustrated. A text figure of the heads alone, showing the distinctive differences in the frontal shield of *Fulica caribaea* and *F. americana* mentioned in the text, would have made more sense than the color plate space given to *caribaea* alone. The addition to the plates of *Butorides virescens* and *Ixobrychus exilis* would have greatly aided field identification of the similar appearing species pairs of which they are both a part. It is the misidentification of these very species in the past that has contributed some of the confusion concerning their present status. The decision not to illustrate birds previously illustrated in field guides for other areas, particularly North America, is expedient, but does a disservice to the non-North American visitors using this book and, more importantly, to the local market on which effective conservation measures depend. Could not at least some of the shorebirds have been illustrated, even if only as a text figure? Also, could not at least a few of the several commonly occurring North American migrant passerines have been squeezed into the plates somewhere?

The plates vary in quality. In several plates space has been used rather extravagantly, possibly at the cost of including additional species. In more than a few cases the margins are wide enough to suggest that the whole plate could have been reproduced substantially larger, using more of the total page area. This would have greatly improved several plates, particularly Plate II, where some of the figures are so small that distinctive differences in the plumage can hardly be seen. My personal familiarity with the birds of these islands leads me to suggest the following changes in the plates: (1) the coloration of *Geotrygon linearis* (Plate VI), *Turdus fumigatus* (Plate XXI) and *Habia rubica* (Plate XXVI); (2) the bill proportions of *Quiscalus lugubris* and *Scaphidura oryzivora* (Plate XXII) and *Ramphocaenus melanurus* (Plate XVI); (3) the deletion of the partial collar in the female of *Cypseloides rutilus* (Plate IX) which as indicated in the text is usually lacking.

Text figures 36 and 37, which were clearly designed to aid in the field identification of the Lineated and Crimson-crested Woodpeckers, would have been more effectively presented on the same page. The captions for these figures appear to be reversed in that the streaked throat mentioned in the text for the Lineated Woodpecker appears in the figure labeled Crimson-crested, while the black throat of the Crimson-crested Woodpecker appears in the figure labeled Lineated Woodpecker.

It would have been a great help to have had page numbers of the species accounts included in the plate captions, and if reference had been made in the captions to the figure or portrait illustrating the other sex to that shown in the plate, or additional species in the same group.

The text is delightfully free of all but a few typographical errors. On the other hand the plates and their captions are a disaster area. In addition to the reversal of text figures 36 and 37, color plates 21 through 28 in my copy are in the improper sequence so that the captions which appear on the facing page are located from one to three pages before or after the appropriate plate. Such a mix-up in the positioning of the plates occurred in two of three copies I examined. The captions also include a case of two species receiving the same scientific name (Large-billed and Lesser Seed-finches, Plate XXVII); the omission of a specific epithet (Bellbird, Plate XII); and eleven misspellings of scientific names (9 plates). These sorts of errors are inexcusable. They are, however, easily correctable in future editions.

Despite these lapses, this book will be wanted by any birder visiting Trinidad and Tobago. Even though a handbook, its size (5 by 7½ inches), weight, illustrations, and price make it equally suitable as a field guide, and it will get its greatest use in this capacity. It will also gain a place on the bookshelf of many ornithologists not planning a visit, simply for the information it contains. As pointed out in the forward, it is all the more to Mr. ffrench's credit "that the very professional text of this book is an avocational work," a view I fully endorse. There is no doubt in my mind that this book will prove to be a superior competitor to previous works considering the avifauna of Trinidad and Tobago.—Charles T. Collins.

American Bird Names. By Ernest A. Choate. Gambit, Inc., Boston, 1973:xv + 261 pp. many bl. and wh. sketches. $6.95.—This is the second book within a year which sets out to give the meanings of the names of North American birds, both common and technical, and to give biographical information about the people whose names have become attached to birds. While flawed in a number of ways it is a much better job than the previous work ("Words for Birds" by E. S. Gruson, see Wilson Bull., 85:521–522, 1973, for a review) and it can be recommended to people who want such information.

In order to write such a book a would-be author must have reasonably authoritative knowledge in the Latin and Greek languages, in philology, in the history of the English language, the history of North America, the history of biology, the history of ornithology, and an understanding of the customs and rules of zoological nomenclature. Besides this formidable list, he must also have a broad knowledge of birds, and particularly of birds in the hand, since this is where most of the terms used in naming were discovered. Such authors will be few indeed (only Elliott Coues comes immediately to mind, and he too made many mistakes). Lacking such exhaustive knowledge mistakes are inevitable, and while Choate comes out better than most people who have made the attempt there are still a large number of errors of fact or interpretation. I will not enumerate these since it would serve little purpose. There are undoubtedly many errors that I am not aware of.

The book consists essentially of three alphabetical lists. The first of these discusses the origins of the so-called "Common Names." Dr. Choate, who is a retired teacher of English, has handled this section quite well, and in particular he has been most thorough in examining the origins of the bird nouns such as "thrush" or "sparrow." The origin of many names is unclear, and in many cases different authorities have advanced alternate

explanations. Choate has carefully dealt with these cases and in most cases he cites his sources. A welcome novelty in this section is the inclusion of the true "common" names (as opposed to the "birdbook" names) of some species. Thus we have such things as "High Hole" and "Blue Peter," but these names are usually only identified and often not explained.

The second section gives translations of the technical names, arranged by genus. In many cases the entry is limited to a simple translation of the several stems in the name, but usually some explanation is given as to why the name was used. The translations are, for the most part, well done, but Choate cannot resist the temptation, seemingly endemic in authors of this sort of work, to editorialize about how inappropriate some names are and to wax a little sarcastic about them. If the name comes out of classical mythology (e.g. *Progne*) Choate frequently relates the myth, often with some rather heavy-handed humor.

The final section gives brief biographical sketches of the people for whom the birds were named. While they serve to identify the eponyms, they are usually too brief to give much information, but, fortunately, they stick to the facts and omit the fanciful stories that so marred the Gruson book.

Choate attempts to keep the nomenclature up to date including the 32nd Supplement to the AOU Check-list (1973—erroneously given as 1953 in the bibliography) but he has overlooked the publication of a BOU Check-list (although not called by that name) more recent than the one of 1952. Choate has a serious misunderstanding about technical nomenclature and the International Code as illustrated by his remarks that actions of the International Commission are only advisory. In three places he attempts to explain the *Gavia-Colymbus-Podiceps* matter, but his three explanations all differ somewhat, and all can only leave the reader confused about what is after all a rather simple situation, now satisfactorily resolved.

In common with others who have written in a similar vein Choate seems to feel that bird names ought to make sense, ought to be appropriate, and ought to be useful. Isn't it time that we recognize that this is an unrealistic idea? Why should bird names make any more sense than the names of people? How many Smiths still work in metal and how many Millers still grind flour? None of my recent relatives have been servants at the lord's manor. These things don't bother us with these names, and why should we worry about such matters with bird names?

The editing and proofreading on the book have been minimal and there are many typos, misspellings, and slips of the pen e.g. "Bibliographical" = biographical; "Larson" = Lesson; and worst of all, the Black-throated Green Warbler is so called because of the "blue-black of the male's plumage."

The book is illustrated with a few woodcuts from Thomas Bewick's, "History of British Birds"—George A. Hall.

A Symposium on the House Sparrow (*Passer domesticus*) and European Tree Sparrow (*P. montanus*) in North America. S. Charles Kendeigh, chairman. Ornithological Monographs No. 14, American Ornithologists' Union, 1973:vi + 121 pp., 25 text figs., paper cover. $3.50 ($2.80 to AOU members. Obtainable from Burt L. Monroe, Jr., Box 23447, Anchorage, Ky. 40223).—The House Sparrow and the Tree Sparrow are, of all free-living birds, the most closely associated with mankind. It is to us that they owe their widespread distribution. Consciously or not, people have taken House Sparrows and, to a lesser extent, Tree Sparrows, with them wherever they went. By transforming

various natural habitats, from the far north to the equator, into an environment affected by human settlements, mankind provided conditions suitable for these sparrows. Within the old range of the House Sparrow in Europe, the spread of development over the land contributes to a prodigious increase in the density of House Sparrow populations. Consequently, in recent years this species has come under the scrutiny of ornithologists and other specialists.

Thanks to the activity of Kendeigh and his disciples in the United States, the House Sparrow has become the model species for many investigations. A Group on Granivorous Birds has been organized in the Section on Terrestrial Productivity of the International Biological Program, for a worldwide study of *Passer domesticus* and *P. montanus*. A symposium for discussion of up-to-date studies on these species in North America was held in 1969 at the 87th meeting of the American Ornithologists' Union at the University of Arkansas. The proceedings of that symposium, comprising 14 reports, have been published as the work here under review.

Chairman Kendeigh opened the symposium with a brief history of the evolution of the genus *Passer* and a discussion of the importance of studies on the House Sparrow. C. S. Robbins then presented a history of the introduction of the House Sparrow into North America, the continental spread of the species, and its present range and abundance.

J. C. Barlow discussed the introduction of the Tree Sparrow into the U.S. from Europe, a very different event from that of the House Sparrow. A few of these birds were brought over from Germany in 1870 and released in St. Louis, Missouri. Within a few years, the species occupied the whole town. As House Sparrows—introduced at the same time as the Tree Sparrows—increased, the latter were forced to withdraw from the central parts of the town, with the result that by the end of the decade, Tree Sparrows inhabited only the suburbs. During the ensuing century, the population of this species increased to 25,000 and occupied an area of 8500 square miles in Missouri and Illinois. This meager increase of the Tree Sparrow was due to competition from the House Sparrow. Barlow also compared color pattern and size between European and American populations of Tree Sparrows.

R. F. Johnston presented his findings on the variability of House Sparrows, focussing on the analysis of sexual dimorphism in the size of bones, particularly those which are associated with the intake of food.

W. Klitz estimated genetic variation in North American House Sparrow populations by electrophoretic detection of allelic differences, and found the birds to be genetically monomorphic.

Four reports dealt with the breeding biology and the movements of House Sparrows: three of these concentrated on the role of the birds in the epidemiology of western encephalitis. The phenology and number of broods, egg losses, and mortality of nestlings were followed, as well as the number of young reared by one pair of parents in a given breeding season.

Four reports continue the classical studies of Kendeigh on various aspects of the bioenergetics of the House Sparrow. C. R. Blem investigated the cold tolerance, insulation, energy balance, and body composition of sparrows collected at eleven different sites from southern Florida to northern Manitoba. He found various forms of acclimatization of the birds to different climatic conditions in the southern and northern parts of their range.

The following reports were published as abstracts: S. C. Kendeigh, "Environmental regulation of food intake by birds." F. H. Blackmore, "Seasonal variation in the energetics of molt in captive outdoor House Sparrows." C. L. Votava, E. W. Martin, and J. W.

Parrish, Jr., "Determination of the low critical partial pressure of oxygen for the House Sparrow," L. B. Barnett, "Seasonal changes in temperature acclimatization of the House Sparrow," and M. H. Clench, "Variability in the body pterylosis of *Passer domesticus* and allies."

This collection of reports includes two original papers published in their entirety—Blem's paper on the geographic variation in the bioenergetics of the House Sparrow, and Klitz's paper on the genetic variability in North American House Sparrows. The abstracts by Kendeigh and by Blackmore present much new and interesting material. The other reports, although not entirely original, supply important data for a current synthesis of the results achieved through the activity of the I.B.P. Working Group on Granivorous Birds.—Jan Pinowski.

Birds of Big Bend National Park and Vicinity. By Roland H. Wauer. University of Texas Press, Austin and London, 1973:xv + 223 pp., col. paintings by Howard Rollin and Anne Pulich. $4.95.—This is a long-needed and useful volume for the legions visiting Big Bend National Park each year. The Park is the U.S. home of the Colima Warbler, and that species alone brings serious birders from afar for one of the southwest's richer avian experiences. With this book Wauer has helped a wide range of naturalists understand the general ecology of the Park and environs as well as locating the sites where life lists might be expanded. There is a fold-out map of considerable detail included for the pilgrim visitor to Big Bend. Two artists contributed color plates: Anne Pulich did the frontispiece of Lucifer Hummingbirds and Howard Rollin prepared a series of groupings framed against characteristic habitats (e.g. Birds of Pinyon-Juniper-Oak Woodlands). Rollin also produced a painting of a Colima Warbler facing the first page of text. This book is available only with durable soft cover in a size that should fit comfortably in the pockets of most field gear.

Big Bend is a land of rugged topography and abrupt altitudinal gradients, and of course these are the features that account for most of the diversity in the plant cover and the attendant avian communities. Wauer accordingly takes the necessary pains to acquaint the reader with the five major plant communities of the Park, including good quality color photographs, with one somewhat blurry exception (pg. 15), of representative habitats.

The importance of this region, and hence the book, can be drawn from the complete historical review of ornithological activity in the Big Bend beginning in 1901 with a summer visit by no less than Harry C. Oberholser, Vernon Bailey, and Louis Agassiz Fuertes. Yet, at Wauer's arrival in 1966, the list for the Park stood at 241 species; some 3500 hours of field work later, the author's list reached 385 species (including 26 hypotheticals)—nearly a 60% increase! Certainly the unique setting of this volume in one of the southwest's more picturesque environments, coupled with an expanded list of this magnitude, warrants treatment in book form. The author makes clear that his work is designed as a "where-to-go-to-find-what" instead of a field guide to bird identity. In this endeavor he has been most successful.

Following three introductory chapters dealing with the area's ornithological history, ecological descriptions of the area, and bird finding (at all seasons) is the main body composed of a 157 page annotated species list. The notes include the usual material on abundance (with definition of terms) and residential status (again, with definitions, pgs. 53–54). The occurrence of the more common species is given by months whereas those more rarely encountered are cited by dates of actual observation. Elevations, and or

other habitat notes are provided as well as specific and colorful site locations (e.g. "Lost Mine Trail," "Panther Junction") where each species has been observed.

Changing nomenclature, the temporal plague of any author, has taken its toll here. The Thirty-second Supplement to the A.O.U. Check-list has rendered several of the species names obsolete in the short period since this book appeared, but this is no fault of the author's, merely a bane to the beginning student.

It is generally difficult to fault this book, and I can do so only with blunted blade. I find certain paintings by Rollin uniformly of less than good quality, although others are certainly well done. However, the lack of perspective and scale between species appearing on the same plate is the most serious drawback, and this alone detracts somewhat from the book's otherwise clear format. There is a transposition of sentences for the Black Hawk material (pg. 75) but this is the only typographical error I located in my examination of the text. I question the need for listing 93 species Wauer found during one 6-hour stint at the peak of spring migration (pg. 35) or the listing of species seen on various Christmas censuses (e.g. "A total of six species were recorded on thirteen of the Christmas counts . . ."; "Eight kinds of birds were recorded on nine of the Christmas counts . . ."; etc. on pages 51–52).

The index includes only the common names of birds, which may be contrary to the desires of some professional readers. In the bibliography (pg. 212) the species name in the title of Hubbard's (1969) paper is misspelled as "*cornota*" instead of "*coronata*." Some literature citations use issue numbers whereas most do not; in one citation (Wauer 1969a) the journal is incorrectly listed as "Bull. of Texas Ornithologists Soc." instead of "Bull. of Texas Ornithological Soc."

But again, these are rather trivial detractions, and ornithologists of every ability will want—and enjoy—this fine book.—Eric G. Bolen.

To Ride the Wind. By H. Albert Hochbaum. A Richard Bonnycastle Book, published by Harlequin Enterprises Ltd., 101 Duncan Mill Road, Don Mills, Ontario, Canada, 1973: 119 pp., 30 color paintings and many black-and-white drawings. $35.00.—This outstanding book on North American waterfowl is in all its aspects a "carriage-trade" item, particularly so its retail price. The book fits no book size dimension (13 × 15 inches) but it comes close to *crown folio* (10 × 15 inches). The odd size is doubtless the result of fitting the colored illustrations to best advantage. There are 30 beautiful colored plates rendered in watercolor and egg tempera, and 40 black-and-white pen or scratch-board chapter vignettes. The paper, printing, and color reproduction are of high quality, but the binding appears weak. I saw a copy in a local bookstore that had become shaky on limited handling.

The preface, foreword and opening essay comprise 14 pages. There follows a three-season (winter omitted) grouping of five essays each. An appendix, including an index of the color plates, a glossary, and a bibliography (with historical annotation) conclude the offering.

The preface is given largely to acknowledgments. H. A. Hochbaum has always generously recognized all minor or tangential assistance in his writings. It was surprising therefore that even faint praise was missing for the major professors from 34 universities who guided the field research of the 77 graduate students that worked out of or at the Delta Waterfowl Research Station.

Sir Peter Scott's foreword is both scholarly and warmly complimentary. He and

the author of the book are firm friends and much alike as artists and waterfowl ecologists. They are a mutual admiration society of two where in each case the admiration is justly deserved.

The text is in story form, simple, informative, colorful, and easy to read. The author's prose is not unlike his painting—many brilliant flashes in a matrix of excellence.

His storytelling embodies unobtrusively all aspects of waterfowl biology including behavior, physiology, and ecology. The Canvasback and the Canada Goose are the two key species used to illustrate the dynamic vitality of waterfowl and the habitats they occupy.

The stories span the years and not all conditions unfolded in the stories hold today. For example, the stubbling flights to grain fields at Delta depicted in words and on canvas are today rare or nonexistent. Grain is still swathed, but the ducks are too few to produce a stubbling flight like those of the early 1950's. Like Ernest Thompson Seton, Hochbaum's narrative is often autobiographical, but nonetheless exciting for being so.

The waterfowl hunter will see himself in Hochbaum's word mirror in Chapter XV. Here too the protectionist will get an insight into the esthetics of hunting and learn of the soul-touching pleasure of wildfowling that some of us are affected or endowed with and how small a role killing plays in wildfowling.

Although crammed with scientific data, this is not a technical publication. There is no mention of confidence limits or correlation coefficients but, if challenged, there is no doubt that the author can quote page and verse to support his statistics.

The book ends on a sad note: the decline of the resource. The author deals at length with the role of the hunter and relatively little with the destruction of habitat, particularly those places where the best may be inadequate. He says (p. 104): "Waterfowl are different [from upland game birds]. Where their reproduction is diminished by drought, ducks, unlike grouse, do not spread their numbers thinly over a broad range. They come together. Even though the flock is not bolstered by a healthy increase of young, the old breeders congregate in the best places, where they make a big autumn show. Ducks are gregarious, as long as there are any at all, they join in flocks, conspicuous and vulnerable."

It is in this context that habitat and hunter must be regulated for the good of the resource and the benefits it produces. Hochbaum openly indicts the agencies responsible for waterfowl welfare as not always making the best judgments in spite of good intentions. His final word on international cooperation concerns the rebuilding of the Migratory Bird Treaty of 1916 between the U.S. and Canada to control ". . . the early-season killing of young ducks and their mothers. . . ."

The message is abundantly clear that the waterfowl resource is confronted with exploitation and loss of preferred habitat to a point where governmental agencies, the private sector, and the hunter himself must work together to preserve the waterfowl resource and perpetuate the sport of wildfowling.

Hochbaum, the artist, is not a calendar painter of pretty pictures; each of his paintings tells a story of time and place in duck ecology. In this regard his brush is equal, if not superior to, his pen. He has a kindred feeling for the moods of prairie skies and the way atmospheric colors play on one another and on his subjects. His birds never appear to be "stuck on" the background as afterthoughts. Most of his paintings deal with the somber colors of spring and fall vegetation against the backdrop of an onrushing sunrise or a deepening afterglow.

The third dimension in his paintings is created by a skillful use of distance perspective (p. 95), and like Francis Lee Jaques he has an understanding of how trees and shrubs are put together (p. 109, my favorite!).

No one will dispute the anatomy of a flying or swimming duck painted by Hochbaum any more than they would dare to question Sir Peter Scott on that aspect of artistic draftmanship.

If I must be critical, then I would have preferred a Greek orthodox church with Byzantine steeples in the prairie town, along with the Quonset architecture of the curling rink depicted in the painting on page 39, and Nan Mulder and I are disappointed that our paper on the history of the Delta Decoy did not rate a bibliographic citation. The black-and-white drawing (page 99) on the shooting of a Canvasback should have been omitted as it does not seem to fit the text or have rapport with the other illustrations.

This is a wonderful book by a superb painter and excellent writer. I said at the outset this was a "carriage-trade" item, and it is. My recommendation: Sell the carriage, and buy the book.—Robert A. McCabe.

Feeding and the Feeding Apparatus in Waders: A Study of the Anatomy and Adaptations in the Charadrii. By Philip J. K. Burton. British Museum (Natural History), London, 1974:150 pp., 41 drawings. £3.50 ($8.40).—This is a careful and detailed analysis of the relationships between feeding habits and the anatomy of the feeding apparatus in shorebirds. Five species of varying habits are emphasized: The Golden Plover, *Pluvialis apricaria*; Redshank, *Tringa totanus*; Curlew, *Numenius arquata*; Dunlin, *Calidris alpina*; and Common Snipe, *Gallinago gallinago*. Field observations were made of their feeding behavior, and descriptions are given of their movements during foraging, including locomotion and various types of pecking and probing for food. These are analyzed quantitatively, as are stomach-content analyses of the foods taken. In this way detailed comparisons between the species is made possible, and the functional significance of both obvious and subtle anatomical differences is illuminated. The feeding of other species of Charadrii is described more briefly, much of it gleaned from the literature.

The anatomical portion of the study is unusually complete. The same five representative species were studied in detail, but comparative dissections are also reported on 118 species of Jacanidae, Rostratulidae, Haematopodidae, Charadriidae, Scolopacidae, Recurvirostridae, Phalaropodidae, Dromadidae, Burhinidae, Glareolidae, Thinocoridae, and Chionidae. Aspects studied include the bill form and length, ligaments, jaw musculature, tongue, hyoid skeleton and muscles, oral epidermis, salivary glands, and those cervical muscles which act on the head. Much of the study is devoted to a correlation of structure with function, including considerations of cranial kinesis, bill orientation, and muscle actions. The adaptive significance of the structural specializations of each form is analyzed much more thoroughly than is often the case in functional-anatomical studies, where behavior of the animals is usually not studied in the detail presented here. Forty-one clear line drawings illustrate the major anatomical features and variations discussed. An interesting innovation is the presentation of cross-sections of entire muscles with the internal aponeuroses clearly delineated and labelled, thus giving a new dimension to the usual presentation of the comparative anatomy of muscles.

Numerous taxonomic comments are scattered through the text, but Burton adopts a cautious approach and refrains from revising the whole group or from presenting a phylogeny of the forms studied. The taxonomic conclusions refer mainly to the proper placement of certain difficult taxa. This caution arises from a clear understanding of the problems of confusing adaptive and phylogenetic bases for morphological similarity;

that is, of distinguishing similarities due to common ancestry with those arising by convergence. A brief discussion of this problem concludes the book. Students of avian functional anatomy, and those interested in the relationships and biology of the Charadrii will find this a thoughtful and scholarly study of feeding adaptations in the shorebirds. —Robert J. Raikow.

The Life of the Hummingbird. By Alexander F. Skutch, with illustrations by Arthur B. Singer. Crown Publishers, Inc., New York, 1973: 95 pp., col. ill. $9.95.—Hummingbirds, as Skutch clearly indicates in this book, have captured the fancy of bird enthusiasts for several centuries. Scientific studies of these birds have lagged a bit behind this popularity. In spite of a recent surge of scientific interest in hummingbird biology, as indicated by the references in the bibliography of this book, Skutch correctly notes that there are still many aspects that are in need of detailed investigation.

The factual material in this book is well-presented and very interesting, although Skutch apparently does not have access to recent work on hummingbird biology that has appeared in non-ornithological publications. Unfortunately, Skutch does not advance hummingbird biology with his uncritical acceptance of behavioral anecdotes. He apparently feels that there is something "special" about hummingbirds that permits flights of fancy in the interpretation of some of their behavior. For example, he tells a story about the interaction of "a" hummingbird and a convalescent man, in which the hummingbird supposedly followed the man on walks, calling his attention to interesting things along the way. Skutch concludes that the bird accompanied "the man because he liked his company." Such statements are not only not very enlightening, but also deflect bird watchers from thinking biologically about their observations. While such a story is "cute" and probably will help sell the book, it certainly is a disservice to readers.

Skutch seems to be sometimes unclear as to the level of sophistication of his anticipated audience. How many readers will know what a manakin is, or how many calories are released when a hummingbird uses one milliliter of oxygen? These criticisms are unpleasant to mention since Skutch has, in fact, provided a fairly modern treatment of much of hummingbird biology.

The artistic talents of Arthur Singer are evident, but some aspects of the figures were hurriedly done. It would have been helpful if plant identifications had been included in the figure legends. In addition, there are specific problems with several figures. The lower hummingbird in the figure on page 45 is not identified in the caption. In the same figure, it is not clear in the line drawing how the bird receives the pollen, since the stamens are not in contact with the bird in the lower picture and there is no indication of the location of the stamens in the upper picture. The caption on page 48 gives an incorrect range for the Long-tailed Hermit, although the range is given correctly on page 76. Careful editing should have removed such slips.

The high cost of the book in relation to the amount of text must represent the cost of reproducing Singer's paintings. In view of the price I cannot recommend this book either for the correct factual material it contains or for its paintings. This is unfortunate because Skutch is one of the few ornithologists actively studying hummingbirds in the tropics, where this extremely interesting group reaches its highest diversity of species, with their accompanying diversity of adaptations. — Larry L. Wolf.

History of the Birds of Kingston, Ontario. Second Edition Revised. By Helen R. Quilliam. Kingston Field Naturalists, 1973:209 pp., 28 photo plates, 2 maps. $4.95 postpaid. Available from The Kingston Field Naturalists, P.O. Box 831, Kingston, Ontario K7L 4X6, Canada.—This monumental little book is an example of the kind of publication to which all regional naturalists' clubs should aspire. Produced inexpensively by photo-offset from typed pages, with a large foldout map that pinpoints all the best bird-watching places, and 16 habitat photographs (including aerial views), this strongly-bound paperback contains a mass of revealing information. We learn that this area at the northeast end of Lake Ontario, 30 miles in radius (the arbitrary limits set to the book), often supports 245 species of birds in the course of a year and that, in historic times, 302 species have been recorded. Though deep in the Great Lakes deciduous forest region, it provides considerable diversity of habitat with extensive woodlands, farms that are reverting to woods, open fields, large numbers of lakes, beaver ponds, and marshes of various kinds. A promontory, Prince Edward Point, protrudes far into Lake Ontario and functions as a funnel through which migratory birds move in great numbers in spring and fall. The Kingston Field Naturalists have made this a special area of study, maintaining teams daily there in some years.

The explorer Samuel de Champlain, the first white man to visit the area, became lost there for several days in the autumn of 1615 while following and trying to identify a bird he had glimpsed. This, author Quilliam notes, is enough to endear him to the heart of all bird-watchers! The scientific study of Kingston birds can be said to have begun when Captain Henry Hadfield, an army officer, worked the area from August 1857 until May 1858. At a time when knowledge of North American birds was still in its infancy, Hadfield produced a number of articles for *The Zoologist*. In the 1890's, two avid naturalists and egg-collectors, the Reverend C. J. Young and Edwin Beaupré, joined forces and kept sets of records. In 1942, a paper on the birds of the area was published in *The Canadian Field Naturalist*.

The Kingston list contains most of the birds that might be expected in this region. About half the total are breeding species and the rest pass through on migration, winter in the area, or are chance occurrences. Thirteen new species have been added since the first (1955) edition of this work. Records show that there are marked fluctuations in abundance of various bird species from time to time, e.g. most pond and diving ducks increased from the time of Beaupré's surveys in the 1920's through to about 1965. The last seven years have shown a slow but sure increase in Shovelers and Gadwalls, with the first nest of the latter being found in 1972. Helen Quilliam's species accounts include historical notes, spring arrival dates, mention of breeding occurrences, and much general information on abundances and habitats. Any observer fortunate enough to have a work such as this to supplement his field guide is off to a flying start. It is hard to imagine any little work more likely to stimulate interest in birds in a regional community.—Allen Keast.

Blackbirds and the Southern Rice Crop. By Brooke Meanley. Resource Publication 100, U.S. Dept. of the Interior, Bureau of Sport Fisheries and Wildlife, Washington, D.C., 1971:64 pp., photographs and maps. Paper cover. $0.35.—"Blackbirds have been a problem to American rice growers since colonial times because man, by his culture of rice, creates food-rich ricefield marshes that apparently are more attractive to blackbirds than the natural marshes in which they have flourished for centuries." So begins this

report on blackbirds and rice-growing in the coastal prairies of Louisiana and Texas and in neighboring states. The major damage to the rice crop is caused by local populations of Red-winged Blackbirds (*Agelaius phoeniceus*), Brown-headed Cowbirds (*Molothrus ater*), Common Grackles (*Quiscalus quiscula*), and Boat-tailed Grackles (*Cassidix major*).

The report first gives information on migration and movements, seasonal numbers, and life expectancy of these birds. Nesting and feeding activities in the region are then described for each species, particularly in relation to rice growing. Rice is shown to constitute about 41 percent of the annual diet of Boat-tailed Grackles and about 46 percent of the diet for the other species, although the percentage of rice varies during the year. Usually a few fields are severely damaged, while most ripening fields are virtually untouched. "The greatest importance of bird damage to the rice crop is therefore the severe and sometimes financially crippling losses suffered by some farmers rather than the average loss over the area" (p. 43).

On the other hand, Meanley gives data which show that these blackbirds also consume large quantities of weedseeds and insects. From the end of harvest until the advent of spring seeding, the rice they eat is but waste grain. Hence, in spite of their depredations, the blackbirds have certain redeeming qualities. The problem for wildlife biologists has been how to assist rice farmers in reducing crop losses without unduly destroying birds or causing hazards to people and the environment. Biologists with the Bureau of Sport Fisheries and Wildlife have studied the problem since 1919, starting with E. R. Kalmbach in Louisiana. The present report is the latest of several on the subject, and is based primarily on Meanley's own investigations over the past twenty years.

He points out that "reducing bird damage is an integral part of rice culture, just as is insect or weed control" (p. 43) and goes on to describe effective methods of avoiding or reducing rice damage—cultural practices, frightening techniques, and trapping to reduce the numbers of blackbirds.

Meanley understands both the predicament of rice farmers and the desirability of not attempting to eradicate the blackbirds. His findings are clearly presented and carefully edited, but the photographs suffer from muddy reproduction and loss of details in the shadows. The report succeeds in providing information to its intended audience of farmers, agriculturists, and biologists about the rice blackbird problem in the South. It is also a good case history for anyone who is concerned about conflicts between wildlife and mankind's use of the land.—Peter Stettenheim.

Birds of the World. Revised Edition. By Paul Barruel. Translated by Phyllis Barclay Smith. Oxford University Press, New York, 1973: 222 pp., maps, 310 photographs and drawings, including 94 in color. $25.00.—"In spite of its title, this book is by no means a 'Birds of the World'. . . ." So wrote Josselyn Van Tyne (Wilson Bull. 67:227, 1955) in review of the first edition. Van Tyne suggested that the French edition's title, "The Life and Habits of Birds," should have been given to the English edition. This second English edition bears the subtitle "Their Life and Habits." Combined with the title, however, this only exaggerates the misnomer. Coverage of the world's birds is in no way intended in this edition either. For example, in the list of families of birds—from which "the less important groups have been omitted"—one finds the Fregatidae, Phaethontidae, and Anhingidae omitted from the Pelecaniformes and the sum total of only 17 families listed under the Passeriformes.

What, then, was the intention of the author? Phrases from the Preface narrow down his objectives: "to present a general picture of the biology of birds": to "make pictures talk"; to "publish a beautiful collection of biological pictures."

There is no doubt as to the book being a collection of pictures. I count (there is no list of pictures in the table of contents) 186 black and white photographs, 86 color photographs, and 8 color plates. A great many of the photographs are indeed beautiful, quite a few would seem to be outstanding. The color plates convey their points vividly.

Five chatty chapters discuss daily activities, reproduction, migration, solitary and gregarious birds, and bird populations. The prose (I have seen only the translated edition) is presumably styled to the audience the book is written for—"as wide a public as possible." Errors in editing are few. The boobies of the color photograph of page 180, despite a bluish tinge which the feet appear to have, cannot be Blue-footed Boobies as captioned. I was unaware of there being "puffins" in Australia (p. 59).

The price of this book may discourage its purchase by the wide public the author professes desire to reach.—Oscar T. Owre.

Populations, Movements and Seasonal Distribution of Mergansers. By A. J. Erskine. Canadian Wildlife Service Report Series Number 17, 1972: 36 pp., photographs, maps, graphs, paper cover. $1.00. (Obtainable from Information Canada, Ottawa, Canada. Catalogue No. CW65-8 17.)—This report is a compilation of data on mergansers (chiefly Common Mergansers) collected between 1957 and 1971. The author summarizes seasonal fluctuations of merganser numbers and movements on northern Cape Breton Island, Nova Scotia and evaluates the impact of systematic year-around shooting on the birds. Although data are presented for a 14 year period, variations in techniques, personnel, and effort limit most of the comparisons to the years 1960 through 1968, excluding 1964. There seems to be a positive correlation between the mean temperature during April and the hatching dates and subsequent fall flocking of young mergansers at bays and river mouths. There is also a significant reduction in the recovery rate of banded mergansers that were marked with nasal discs. The author points out a major weakness; no one set of data is complete for the entire study. To compensate, observational information is presented, but this tends to confuse and complicate the report and the findings. One conclusion is clear; year-around shooting of mergansers to reduce fish mortality within a watershed can significantly reduce the number of mergansers without having much effect on nearby watersheds. More data concerning merganser numbers after termination of shooting would have been desirable. The limited information suggests that repopulation may be slower than predicted. Although the impact of year-around shooting was one of the major objectives of this study, no data are presented concerning the total number of mergansers shot. The small samples and variable design also limit the statistical analyses that can be done. The author suggests that the 6 week span of merganser hatching dates is similar to that of other renesting species. Yet, based on his observations of Buffleheads, he states that mergansers probably do not renest. This conclusion ignores other cavity-nesting waterfowl species that do renest, such as Wood Ducks. More data on mergansers are necessary to resolve this conflict. The illustrations in the report are helpful and well done. The report is a good review of the literature published on mergansers.—Harold H. Prince.

CONSERVATION SECTION

CONSERVATION COMMITTEE REPORT ON STATUS OF EAGLES

Bald (*Haliaeetus leucocephalus*) and Golden (*Aquila chrysaetos*) eagles historically occurred in suitable habitats throughout the U.S. and Canada. With settlement, populations of eagles came into conflict with man principally through man's use and alteration of habitats necessary for maintenance of eagle populations. Such conflicts increased in the 1900's. Consequently, the food base of eagles was altered, food chains were contaminated by pesticides, preferred nesting areas were destroyed or otherwise rendered unusable, and attractive (to eagles) hazards were placed in areas historically used by them. Because of widespread publicity about deaths of eagles in recent years the Conservation Committee of The Wilson Ornithological Society undertook the task of reviewing the present status and problems of eagles in North America. Major problems encountered with management of eagles are:

1. Maintenance of suitable nesting and feeding habitats
2. Reduction of man-caused mortalities
   a) Poisoning
   b) Shooting
   c) Electrocution

HISTORICAL RÉSUMÉ

In North America, man has historically attempted to reduce or eliminate eagles whenever conflicts have arisen in use of commodities desired by man. These conflicts have been most intense and widely publicized in situations where eagles (primarily Golden) have preyed, or have been alleged to prey on domestic livestock. Numerous articles containing both fact and fiction have been written concerning eagle-livestock problems in western North America. Because of alleged and actual predation on young livestock (principally sheep and goats) by eagles, ranchers have made concerted efforts through shooting and poisoning to reduce or eliminate eagles and other large birds of prey from their livestock ranges. Other problems have arisen through destruction of cliff and tree nesting sites used by eagles, reduction of the amount of foraging area near nest areas, release of pollutants into the environment which can cause either death or reduction of reproductive ability, erection of power poles without proper safeguards against potential electrocution, and casual shooting for sport and sale of feathers. Bald Eagles have had legal protection in most areas since 1940, while Golden Eagles were essentially unprotected over major portions of their range until the early 1960's.

PRESENT STATUS

Bald Eagles still occupy most if not all of their historic range although most state conservation departments and knowledgeable individuals contacted report far fewer Bald Eagles than were believed to have occurred historically. Major changes in reproductive performance of Bald Eagles have occurred in some areas, especially in the eastern and southeastern U.S., since the late 1940's. Recent data indicate that the downward trend in reproductive success has slowed if not stopped. In the upper midwest,

Canada and Alaska, all indications are that Bald Eagles are doing well in nesting success and fledging of young. While accurate data on numbers of Bald Eagles are lacking for many areas, approximately 1,000 nesting pairs occur in the lower 48 states with a great many more in Canada and Alaska. It is probable that the continental population of Bald Eagles is between 35,000–60,000 birds, most of these occurring in Alaska and Canada. Bald Eagles have been legally protected in the U.S., except in Alaska, since the Bald Eagle Act of 1940. Overall direct man-caused mortality of Bald Eagles has decreased primarily because of eliminating bounties on them in Alaska; it probably accounts for fewer than 500 Bald Eagle deaths each year. This reduction in the loss of eagles in Alaska has been partially offset by increased habitat alteration and food contamination with pesticides south of the international boundary with Canada.

Populations of Golden Eagles appear to be sizable, reproductively healthy, and stable over much of their historic range west of the Mississippi River. East of this area, few Golden Eagles persist. They are essentially extirpated in the eastern U.S., apparently as the result of loss of suitable foraging areas due to fire control and intensive agriculture.

Attempts to reduce, eliminate or control Golden Eagles have occurred in localized areas where raising of sheep and or goats are important. These control efforts were common prior to 1963, when Golden Eagles were given additional protection under the amended Bald Eagle Act. Efforts to control eagles continued even after this date in some western states under special provisions of the 1963 law. With the disclosure of substantial numbers of eagle deaths through aerial shooting and poisoning in the early 1970's, federal and state agencies increased their surveillance of eagles with the result that illegal killing of eagles in western North America may be at its lowest level since 1900.

With interest in eagles at a high level, another major mortality factor for eagles (primarily young just learning to fly) was identified in the early 1970's. Electrocution of Golden Eagles (mostly) is apparently not recent in origin but has become more common with the advent of increased numbers and kilometers of power lines. Fortunately, not all power lines are harmful to eagles and recent research has provided several solutions to this problem. Most utility companies, eager to improve their public relations, are modifying their line attachment to poles whenever problems with eagle deaths are reported to them. Despite these problems and those associated with reduced foraging areas due to increased urbanization and irrigation, and casual shooting of any large bird of prey, Golden Eagles are holding their own and it is estimated that up to 100,000 individuals occur in North America.

SUMMARY

Populations of eagles in North America have been substantially reduced in many areas of their former range. This is especially true for both species of eagles in the eastern U.S. Major reasons for reduction in populations are related to habitat alteration, contamination of foods with pesticides, and shooting. Populations of eagles breeding in Alaska, Canada and the western U.S. appear to have been little affected although substantial man-induced mortality has been documented. Continental populations of Bald Eagles may be as high as 35,000–60,000 individuals with a North American population of up to 100,000 Golden Eagles. Major problems still remain in order to maintain eagle populations in the 48 contiguous states. This is especially true for the Bald Eagle. Identifiable threats to stable eagle populations are: loss of feeding and nesting sites due to man's activities, pesticide contamination of foods, illegal shooting in areas devoted

to sheep and or goat ranching, electrocution, and shooting for commercial and "sporting" reasons. Due to publicity about deaths of eagles and increased awareness of values of all raptors, federal and state agencies have made commendable efforts to decrease illegal shooting of eagles and to increase their knowledge concerning numbers and biology of eagles and other birds of prey.

For specific detailed data from which this report was prepared, contact Dr. C. E. Braun, Wildlife Research Center, P.O. Box 2287, Ft. Collins, CO 80522.

RECOMMENDATIONS

1. Federal and state agencies should identify and protect all concentrations of nesting eagles on public lands. Where unusual nesting concentrations occur, it may be desirable to establish refuges for the protection of nesting birds. Locations of eyries should not be publicized.
2. Utility companies should be encouraged to eliminate all hazardous perches on transmission lines.
3. Increased research should be supported by livestock interests in order to ascertain exact cause of death of newly born lambs and kids in herderless pastures.
4. Education of sportsmen and recreationists concerning the value of large raptors must be given major emphasis by federal and state land management and conservation agencies.
5. The ban on use of toxic substances such as thallium and sodium monofluoracetate (1080) must continue on public lands. If other alternatives are not available, use of poisons should be carefully controlled and supervised by trained personnel.
6. Traps used in capture of predatory animals should be modified to prevent crushing of the legs of eagles and other raptors.
7. Efforts to reduce and eliminate contamination of the environment with persistent pesticides should be continued.
8. Hunting any wildlife by plane should be outlawed. Pilots convicted of aiding in the molesting of federally protected species such as eagles should have their license suspended or revoked by the Federal Aviation Administration.
9. Ranchers who lease public lands for grazing and who are convicted of molesting raptors should have their lease applications denied by the responsible state or federal agency.
10. Additional research should be conducted in determining the origin of wintering eagles, especially in the western U.S.
11. Where eagles have been extirpated, introduction techniques should be researched and implemented.
12. Where large concentrations of nesting raptors exist, efforts should be made to maintain significant portions of the plant-animal communities in a "natural" (relatively undisturbed) condition. This will help insure that appropriate prey species are available to the raptors.

ACKNOWLEDGMENTS

This report could not have been possible without the cooperation of state and provincial conservation departments. We were also allowed access to unpublished reports of the U.S. Forest Service, U.S. Fish and Wildlife Service, and Bureau of Land Manage-

ment for which we are grateful. J. M. Gerrard and R. W. Nero provided access to published and unpublished reports concerning eagles in Canada. J. Grier and M. Kochert allowed us to review unpublished manuscripts which greatly facilitated preparation of this report. Dr. J. R. Murphy of Brigham Young University reviewed the initial draft and made constructive suggestions for its improvement.

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Tables.—Tables are expensive to print and authors should consider carefully whether or not a table is really necessary or adds to the paper. Tables should be designed so as to be narrow and deep rather than wide and shallow. Double space all entries in tables, including titles. Do not use vertical rules. Tables should be typed on separate sheets and placed at the end of the MS.

Figures.—All illustrations should be prepared (particularly insofar as the lettering goes) so as to be readable when reduced in size. The final size will usually be 11.4 cm wide. Illustrations larger than 22 × 28 cm will not be accepted, and these should be reduced photographically before submitting. Legends for all figures should be typed on a separate sheet. Photographs should be clear, of good contrast, and on glossy paper. Drawings should be in India ink on good drawing board, drafting paper, or blue-lined graph paper. All lettering on drawings should be done with a lettering instrument or the equivalent. Designate the top of each illustration and identify (on the back in soft pencil) with author's name, and figure number. Submit 2 duplicates or readable xerographic copies of each figure so that originals don't have to be sent to the reviewers.

Style and Format.—For general matters of style in preparing a scientific article authors should consult the "CBE Style Manual," 3rd Ed., Am. Inst. Biol. Sci., Washington, D.C. 1972. All MSS should be submitted in the general format used in recent issues of the *Bulletin*. Avoid footnotes, and avoid more than 2 levels of subject subheadings. Except in rare circumstances lead papers should be followed by a summary, not to exceed 10% of the length of the paper. Summaries should be informative when standing by themselves. Most units should be given in the metric system, and compound units should be given in one-line form (i.e. $cm\text{-}sec^{-2}$). The continental system of dating (21 March 1972) and the 24 hour clock (09:00 and 22:00) should be used.

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This issue of *The Wilson Bulletin* was published on 26 March 1975.

THE WILSON BULLETIN

Editor JEROME A. JACKSON
Department of Zoology
P.O. Drawer Z
Mississippi State University
Mississippi State, MS 39762

Editorial Assistants ROBERT J. ESHER
DAVID F. WERSCHKUL

Review Editor ROBERT RAIKOW
Department of Biology
University of Pittsburgh
Pittsburgh, PA 15213

Color Plate Editor WILLIAM A. LUNK
865 North Wagner Road
Ann Arbor, MI 48103

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The Wilson Bulletin

PUBLISHED BY THE WILSON ORNITHOLOGICAL SOCIETY

VOL. 87, NO. 2 JUNE 1975 PAGES 145–302

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The official organ of the Wilson Ornithological Society, published quarterly, in March, June, September and December. The subscription price, both in the United States and elsewhere, is $10.00 per year. Single copies, $2.50. Subscriptions, changes of address and claims for undelivered copies should be sent to the Treasurer. Most back issues of the *Bulletin* are available (at $2.50 each) and may be ordered from the Treasurer. Special prices will be quoted for quantity orders.

All articles and communications for publications, books and publications for reviews should be addressed to the Editor. Exchanges should be addressed to The Josselyn Van Tyne Memorial Library, Museum of Zoology Ann Arbor, Michigan. Known office of publication: Department of Zoology, Mississippi State University Mississippi State, Mississippi 39762.

Second class postage paid at Mississippi State, Mississippi and at additional mailing office.

PRINTED IN U.S.A. Allen Press, Inc., Lawrence, Kansas 66044

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Representative *Passerina* from the Plains. Top: "pure" Indigo male from Niobrara, Nebr. Middle: two presumed hybrid males from Chadron, Nebr. Bottom: "pure" Lazuli male from Shoshor

THE WILSON BULLETIN

A QUARTERLY MAGAZINE OF ORNITHOLOGY

Published by the Wilson Ornithological Society

VOL. 87, NO. 2 JUNE 1975 PAGES 145–302

A BEHAVIORAL AND MORPHOLOGICAL STUDY OF SYMPATRY IN THE INDIGO AND LAZULI BUNTINGS OF THE GREAT PLAINS

STEPHEN T. EMLEN, JAMES D. RISING, AND WILLIAM L. THOMPSON

Eastern and western counterpart taxa (species and near-species) in several avian genera meet and interbreed in the Great Plains of North America (Sibley 1961, Mengel 1970). Among these are the Lazuli Bunting (*Passerina amoena*) of the west and the Indigo Bunting (*P. cyanea*) of the east. Information on the interactions of these buntings in the Plains region was largely anecdotal until studied by Sibley and Short (1959) in South Dakota, Nebraska, Kansas, Colorado, and Wyoming. From this study, which showed that a number of specimens from the Plains were intermediate in plumage, Sibley and Short concluded that hybridization between the forms was common. Nonetheless, as conclusive evidence of extensive introgression between the species was lacking, they (1959:461) suggested that final assessment of the evolutionary status of the 2 *Passerina* required more information on ". . . pairing, mate-selection, and habitat preference of the two forms in the area of hybridization and overlap."

Field studies of sympatric populations of closely related forms are of interest because they permit assessment of the "interspecific" roles of cues used primarily for "intraspecific" communication. The *Passerina* are ideal for such studies: the males are strikingly different in appearance, and are easily separable in the field; the songs differ both in structure and cadence, and the importance of these parameters has been well documented (Thompson 1968, 1970, Emlen 1972); the agonistic and courtship behavior of these birds is well understood (Thompson 1965, Emlen 1972) making it possible to interpret both interactions between birds in the field and responses of individuals to song playback experiments. Field observations on habitat separation and territory overlap can provide additional information on the ecological similarity of sympatric forms.

If mating among the buntings is non-random, the situation would be especially intriguing since one feature commonly believed to mediate gene flow is song, and previous studies have shown that details of *Passerina* song are learned (Rice and Thompson 1968, Emlen 1972). We thus could examine the evolutionary significance of a "cultural" trait in determining gene frequencies.

With these objectives, we examined both "mixed" and "pure" bunting populations, looking for patterns of variation in morphology, ecology, song, and behavior. Our results permit us to speculate on the significance of song for recognition (and thus potentially for species segregation), on the duration of the critical periods for learning the utterance and recognition of song, and on the relative frequency and success of mixed matings. This, in turn, yields a better understanding of the selective pressures in operation and of the current status of bunting evolution in the Plains.

MATERIALS AND METHODS

Study localities.—The Niobrara River in northern Nebraska flows west to east through a region where the ranges of Indigo and Lazuli buntings overlap. From 22 June through 4 July 1969 we examined 3 populations near Niobrara, 3 near Valentine, and 2 near Chadron, all along the Niobrara in Nebraska, and 1 population west of the Niobrara drainage, near Shoshoni, Wyoming (Fig. 1). Thompson obtained additional song data on Indigo Buntings from Iowa, and on Lazuli Buntings from Colorado.

Our 3 study sites in Knox Co. were: 6.6 km N Niobrara; 15 km W Niobrara; and .8 km S Verdel. The dominant arboreal vegetation was cottonwood (*Populus* cf. *deltoides*), elm (*Ulmus americana*), and willow (*Salix* sp.), with ash (*Fraxinus* sp.), oak (*Quercus macrocarpa*), and box elder (*Acer negundo*) also present. The understory was sparse, and the buntings were found along field–woods interfaces.

In Cherry Co. we studied buntings at Fort Niobrara National Wildlife Refuge, 21.7 km E Valentine; .8 km N Valentine, along Minnechaduza Lake and Creek; and 50 km west of Valentine, 13.3 km S Nenzel. The predominant trees were cottonwood, elm, ash, and willow. Oak and box elder were also present. North of Valentine, along north-facing bluffs facing the Niobrara, the vegetation was rank and included such species as birch (*Betula papyrifera*), hornbeam (*Ostrya virginiana*) and pine (*Pinus ponderosa*), attesting to the more xeric nature of such areas. Underbrush was short, due in part to grazing and, just north of Valentine, to a city park. Buntings were abundant and held territories along the woods–field edge.

In Dawes Co. we studied buntings 10 km S Chadron, adjacent to a small reservoir and creek; and 10 km ESE Chadron, along Little Bordeaux Creek. The former site was more mesic, with tall cottonwoods and willows, some ash, and rank understory. The Little Bordeaux Creek locality was overgrazed, with significant understory restricted to draws where plum (*Prunus*), nettles (*Urtica*), ragweed (*Ambrosia*), and daisy fleabane (*Erigeron*) were common. Scattered ash, elm, and willow grew in open stands.

In Wyoming, our study site was 30 km N Shoshoni, along the Wind River. The buntings were found in a narrow band of trees (primarily cottonwoods) with spear grass (*Stipa*) understory, bordered by sage (*Artemisia*).

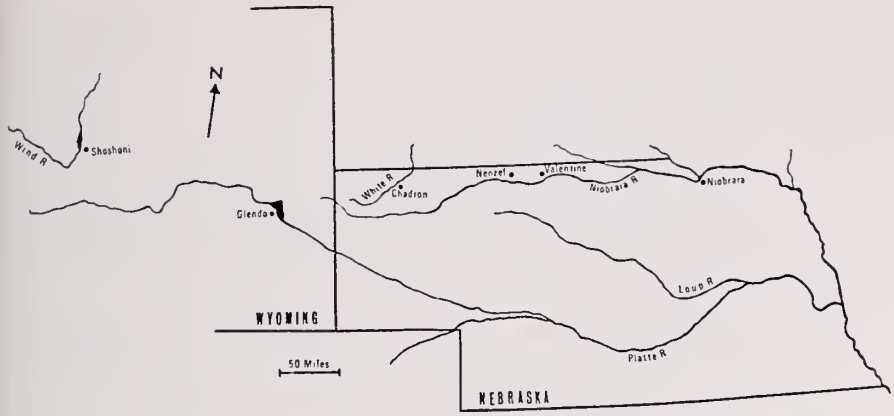

FIG. 1. Localities (mostly along the Niobrara River) at which *Passerina* were studied in 1969: Niobrara, Nebraska (23–25 June); Valentine, Nebraska (25–28 June); Chadron, Nebraska (29–30 June); Shoshoni, Wyoming (1 July).

Study of song.—At each locality, Thompson recorded the songs of territorial male buntings using a Shure 545 Unidyne III dynamic microphone and a Uher 4000 Report-S tape recorder at a speed of 7-½ i.p.s. (19 cm p.s.). Several songs were recorded for each bird, and one judged to be typical was selected for detailed analysis.

Sound spectrograms were made with a Kay Electric Company model 6061-B Sona-Graph, using the high shape and wide band settings. Four song features were examined in detail: 1, *figure morphology*—the detailed structure of the individual song figures; 2, *repetition index*—a measure of the tendency for song figures to be repeated in pairs or triplets, and defined as the total number of figures in a song divided by the number of different types of figures; 3, the *frequency of buzzes* in the song; and 4, *temporal intervals* between successive figures within a song.

Song features of populations from the main study localities were compared with one another and with song data from Indigo Buntings in Michigan (Thompson 1968, 1970) and New York (Emlen 1972) and Lazuli Buntings from Utah and Pacific states (Thompson 1968). Since songs of Indigo Buntings from Knox and Cherry cos. showed no significant differences from more eastern populations, these data were pooled for some of the analyses. Similarly, for certain analyses, songs of Lazuli Buntings from Shoshoni and Colorado were pooled with those of more western populations.

In the analysis of figure morphology, song figures of birds of *P. cyanea* or intermediate plumage were compared with the catalog or "dictionary" of figures compiled from eastern populations published earlier (Thompson 1970). Thompson compiled a catalog of *P. amoena* figures using songs from birds far west of any reported zone of sympatry. This catalog, which will be published separately, was used for comparison with the *P. cyanea* catalog, with the songs of *P. amoena* (by plumage) from along the Niobrara, and with the songs of males with intermediate plumage.

Study of behavior.—Emlen gathered data on territorial behavior of males and performed playback experiments to determine each individual's responsiveness to Lazuli and Indigo song types. At each locality, sketch maps were made of the territories of singing

males, and notes kept of all border encounters and male–female interactions observed. At Chadron, we made a special effort to locate and collect females with mates and to determine the stage of breeding of such pairs.

For playback experiments, we used a Uher 4000-Report L tape recorder, a Nagra DH portable amplifier, and an Atlas WT-2 speaker connected to the amplifier by 30.5 m of cord.

The test songs were recorded from birds outside the zones of sympatry. The Indigo Bunting song used was from a bird recorded in Tompkins Co., New York; the Lazuli Bunting song was a recording made in central California. Each test tape contained the single song (Fig. 2) repeated at 12 sec intervals, a singing rate well within the typical range for *Passerina*.

Each bird was exposed to both test songs and the results were compared by a paired statistical test. This decreases variance caused by extraneous factors such as differences in responsiveness at different stages in the reproductive cycle, or inter-individual differences in the quality of response. In the areas of allopatry, the test song of the unlike form was presented first; in zones of possible sympatry (Valentine and Chadron) the sequence of presentation was randomized. If the first test song produced no response, the second song was played after a pause of 10 to 30 min. If the territorial male showed any sign of responding to the first test, the second test was conducted at approximately the same time on the following day. We took this precaution because previous experiments with *P. cyanea* have shown that the birds habituate to repeated song playback (Emlen 1972).

We initiated experiments only when the territorial male was known to be in the vicinity of the speaker. In practice, the speaker was placed on the ground directed upward near the presumed center of a territory or adjacent to a principal song perch. The tape recorder was turned on and the test song allowed to play for a period of 3 min measured from the time the bird made its first response to the playback. If no response occurred after continuous playback for 6 min, the experiment was terminated and given a zero score.

If the bird did respond, detailed notes were taken of its behavior during the 3 min of playback and 6 min immediately following playback. The behavior was scored according to 2 predetermined scales of responsiveness. The first evaluates the maximum intensity of the response on a scale ranging from 0 (no reaction) through a graded series of "alarm," "approach," and "attack" responses, to a value of 7 (a fully submissive response to the experimental song). In the second scale, each of 8 components of the agonistic repertoire is scored separately (as 0, 1, or 2) according to its frequency of occurrence. These values then are summed to give a 0 to 16 scale which is less dependent upon the subjective weighing of one posture or call over another. (Details of the derivation of these scales and arguments of their relative merits may be found in Emlen 1972.) The data were compared by the Wilcoxon Matched-Pairs Sign-Rank Test (Siegel 1956).

Morphological study.— Rising collected specimens at each locality, making a special effort to collect individuals for which we had obtained playback observations. Fifty-three buntings (all adults) were collected: 5 definite pairs, 34 other males, and 9 other females. Study skins of these specimens are at Cornell University (CU nos. 34218 to 34270). All these birds were in presumptive breeding condition (males with testes enlarged; most females with oviducts and/or ova enlarged, or a brood patch present).

In the analyses, these 53 bunting specimens, plus those collected by Sibley and Short (1959) and a few specimens from the University of Kansas Museum of Natural History

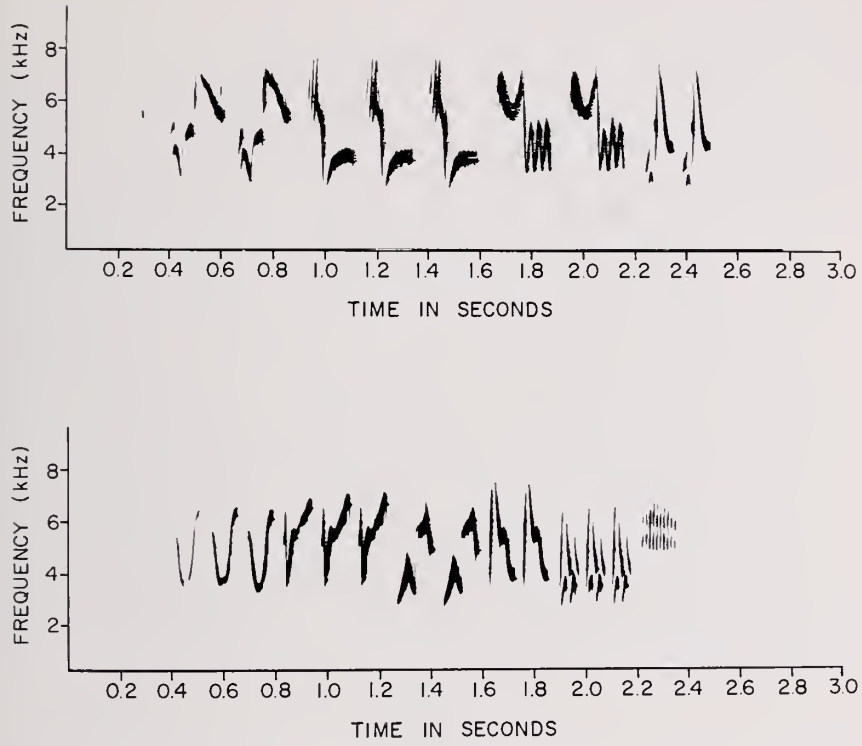

FIG. 2. Test songs of Indigo Bunting (top) and Lazuli Bunting (bottom) used in song playback studies.

(KU) comprise the "Plains sample." To provide standards against which these Plains specimens could be viewed, random sets of Indigo Buntings from Ontario and New York, and of Lazuli Buntings from British Columbia, California, and Utah were examined from the collections at Cornell University and the Royal Ontario Museum (Toronto).

Variation in color and pattern was assessed by use of subjective multistate categories (Appendices 1 and 2). Some of the characters used to assess differences in coloration reflect variation in the blue colors which apparently can be dietarily influenced (Emlen pers. obs.). Nonetheless, these features (forehead, throat, and rump color) can consistently be used to separate wild-taken specimens of the basically cobalt-blue Indigo Bunting from the turquoise-blue Lazuli Bunting. In assessing the blue of specimens, long series (including eastern and western reference birds) were laid out under the same fluorescent lights. The range of coloration within the eastern reference birds was taken to be representative of that of Indigo Buntings, and that of western birds as representative of Lazuli Buntings. Each of the specimens from the Plains sample was compared against the standards and scored according to the criteria in the appendices.

We measured the chord of the longest unflattened wing feather, length of the longest rectrix, tarsal length (diagonal distance between the tibiotarsal–tarsometatarsal joint and

the last undivided scute), length of the horny bill (anterior edge of the nostril to the tip), and the bill width (greatest width of the upper mandible).

We pooled the 5 mensural and 6 plumage characters and analyzed overall phenetic variation using principal components analysis (PCA) based on the matrix of correlation coefficients among the 11 characters (Sneath and Sokal 1973:245–247; for a fuller discussion of multivariate techniques and their use in studies of this type, see Rohwer 1972). First-year males (which can be identified by the color of the primary covert feathers) were not analyzed by PCA since assessment of abdomen color, and often of other features, is impossible. For the females, the matrix of 5 measurements and 3 color features was similarly analyzed. This multivariate procedure is useful for arranging or ordering the individuals along uncorrelated (orthogonal) axes, simultaneously considering variation in all the characters among all the individuals. A weakness of this approach is that discrimination is not maximized, so we also analyzed these matrices using discriminant function analysis (DFA), another multivariate technique (Sneath and Sokal 1973:400–405), using the following as reference samples: 27 males from New York and Ontario versus 27 males from British Columbia, California, and Utah; and 18 females from Ontario versus 11 females from British Columbia and California. For DFA only the 5 mensural features were used, thus giving an estimate of phenetic separation that is independent of plumage characteristics, and permitting the inclusion of first-year males. In both PCA and DFA analyses, missing mensural data (e.g., features that were broken and could not be measured) were estimated by regression analysis using the other measurement that best predicted the size of the deleted characteristic. There were no missing features in the reference samples, and not more than one for any other specimen. Specimens missing plumage character index values were not used in PCA.

RESULTS

Morphology

Both the PCA and the DFA clearly separate the Plains buntings into 2 clusters that correspond to nominant Indigo and Lazuli buntings (Figs. 3, 4, 5, and 6). In the PCA plot for males (Fig. 3) several of the specimens from Nebraska and Colorado fall between the reference Indigo and Lazuli clusters that separate along the component 1 axis, apparently reflecting differences in wing, tail, and culmen lengths in addition to the plumage color features. Of these, birds C, D, and N are clearly intermediate in plumage. Birds B and M may also be intermediate, but are close to Lazuli, and G, H, and E are perhaps intermediate, but close to Indigo. Birds A, J, and O all appear by eye to be of Lazuli plumage, and F, L, and K all appear by eye to be Indigo Buntings. None of the females is intermediate on the PCA plot (Fig. 4).

Insomuch as there is considerable subjectivity involved in assigning the character index scores and possible circularity in interpreting them, we sought to discriminate further between the buntings using DFA based *only* on the 5 mensural features. These features discriminated between the reference samples with but slight inconsistency or error: 1 of the 27 (3%) reference

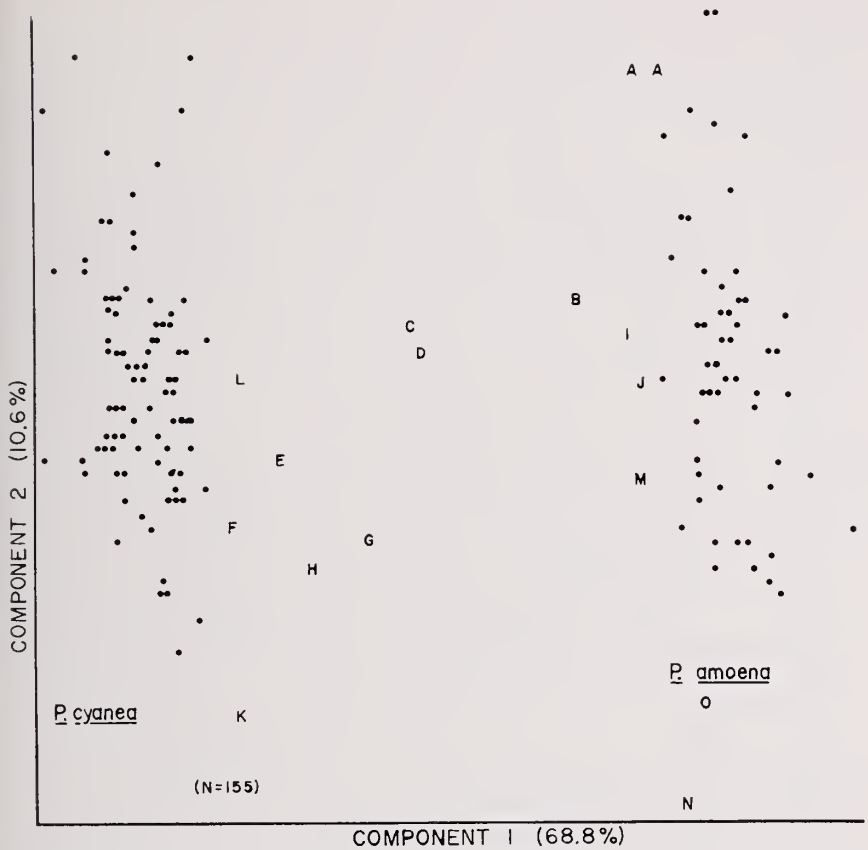

FIG. 3. A 2-dimensional view of the phenetic position of 155 male buntings on principal components 1 and 2 extracted from the matrix of correlations among 11 characters. Together, components 1 and 2 account for 79.4% of the total variance. The letters indicate the position of specimens singled out for discussion in the text: **A**, Shoshoni, Wyo. (1969); **B**, CU 25516, 10 km ESE Chadron (1955); **C**, CU 34251, 10 km S Chadron (1969); **D**, CU 27395, Crook Co., Colo. (1955); **E**, CU 27392, Crook, Colo. (1955); **F**, CU 27612, Blair, Nebr. (1955); **G**, 34257, 10 km S Chadron (1969); **H**, CU 27401, Goodrich, Colo. (1955); **I**, Royal Ontario Mus. 70815, Nicasio, Calif.; **J**, CU 25505, 15 km ENE Valentine, Nebr. (1955); **K**, ROM 72898, Cobourg, Ont.; **L**, CU 25501, 15 km ENE Valentine (1955); **M**, CU 27396, Goodrich, Colo. (1955); **N**, CU 34247, 10 km S Chadron (1969); **O**, CU 34245, 10 km ESE Chadron (1969). All birds collected in 1955 are from Sibley and Short (1959).

Indigo males could not be separated from the Lazuli males; all of the Lazuli males could be discriminated from Indigo males; all of the reference females were correctly differentiated (Figs. 5 and 6). The histogram of the discriminant scores of all male birds from the Great Plains (obtained by multiplying

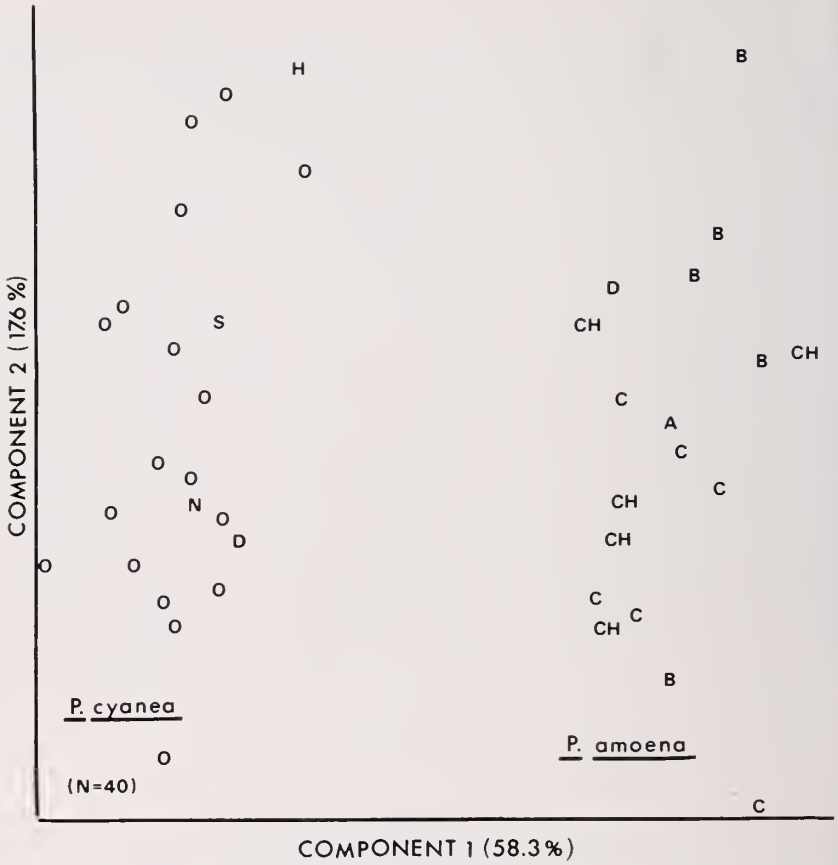

FIG. 4. A 2-dimensional view of the phenetic position of 40 female buntings on principal components 1 and 2 extracted from the matrix of correlations among 8 characters. Together, components 1 and 2 account for 75.9% of the total variance. The letters refer to the following localities: **A**, 10 km SE Chadron (1955); **B**, British Columbia; **C**, California; **D**, 10 km ESE Chadron (1969); **CH**, 10 km S Chadron (1969); **H**, 25 km E, 25 km S Hoxie, Sheridan Co., Kans.; **N**, 13.3 km S Nenzel, Nebr.; **S**, 6.6 km N, 1.6 km E St. Francis, Cheyenne Co., Kans.; **O**, Ontario.

each measurement by its discriminant weight (Appendix 4) and obtaining a single value for each specimen to indicate its position) shows the scores to be distributed roughly bimodally. About 5% of the male specimens are "misidentified" (i.e., are placed differently than their plumage features would indicate), a percentage similar to the number misidentified in the reference samples. The DFA (Fig. 5) suggests that there has been a shift toward Indigo-like buntings at Valentine since 1955—as indeed the plumages of the

buntings suggest. Four of the 6 birds (from the total 101) that are "intermediate" on the DFA were taken at Little Bordeaux Creek, 10 km ESE Chadron; these specimens all appear by eye to be Lazuli Buntings. However, all but one are first-year males and thus it is hard to assess their plumage features accurately. None of the birds that appears to be a hybrid on the basis of plumage is intermediate on the DFA. Thus, while there does appear to be some independence of plumage and size of the males, both the PCA and the DFA suggest that only a few specimens from the Plains fall outside of the phenotypic ranges of Indigo and Lazuli buntings. The DFA additionally suggests that the plumage patterns have not been grossly misinterpreted: the basic Indigo-Lazuli separation is preserved, with relatively few individuals intermediate.

None of the 11 females from the Plains falls outside the statistical limits of reference Indigos or Lazulis. But 5 specimens are close enough to deserve mention. Three, all from 10 km S Chadron, have "borderline" *P. amoena* scores (CU 34255, 34258, and 34263). These all appear to be typical Lazuli Buntings by plumage and cluster with Lazuli females in the PCA (Fig. 4). The fourth specimen (CU 34246) taken at Little Bordeaux Creek scored as a borderline Indigo by DFA but was identified as a Lazuli by PCA and plumage inspection. The 5th female (KU 54644) was collected in Sheridan Co., Kansas in 1966. It clustered with Indigo Buntings by PCA and plumage, yet fell within the Lazuli range by DFA.

The small numbers of female specimens make it difficult to interpret these results although they suggest, as with the males, some independence of plumage and size. The distribution of discriminant scores of the 11 females from the Plains is unimodal (Fig. 6); most of the "intermediate" specimens are from the Chadron region (plus KU 54644), and could well be of mixed parentage.

Song Variation

Song figures.—East and west of the zone of sympatry (Chadron, Nebraska), buntings sang Indigo or Lazuli song figures which were essentially the same as those of birds from populations in the main parts of their respective ranges. The 31 Indigo Buntings from eastern Nebraska and Iowa sang a total of 63 song figure types of which 49 matched up perfectly with counterparts in Thompson's (1970) catalog of *P. cyanea* songs from Michigan. Thirteen additional figures were variants showing only slight differences from those described previously. Only one song figure was so distinctive that it could not be identified with a counterpart from the Michigan population, and it seems to represent a composite of 2 Michigan figures.

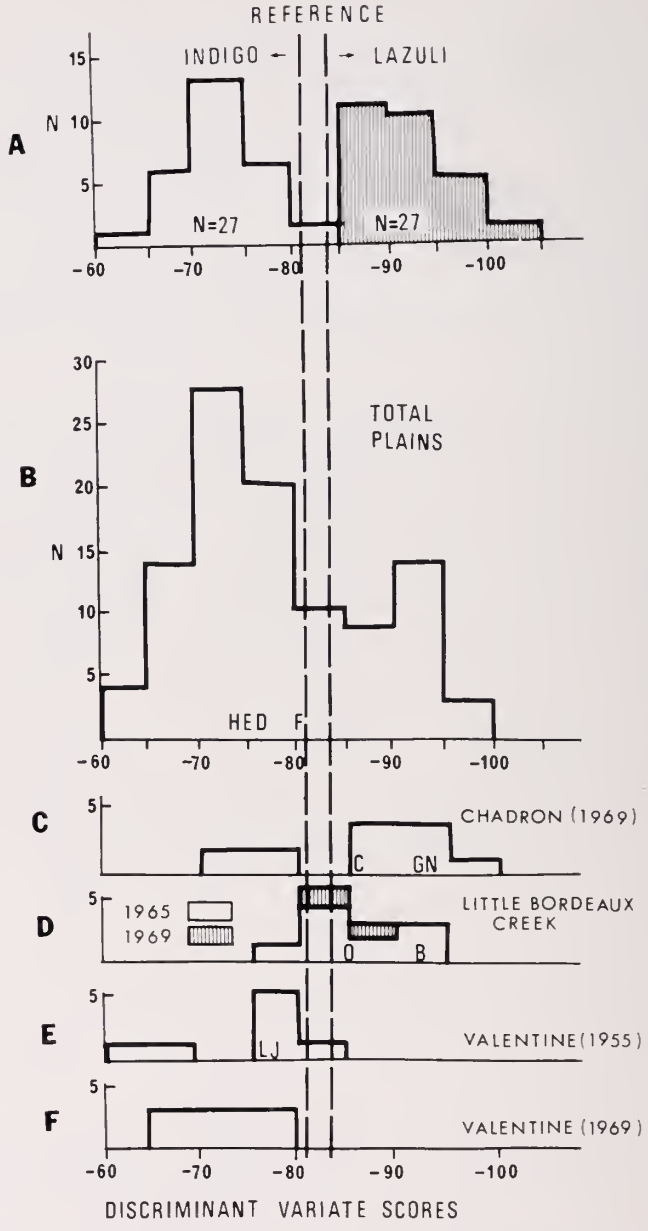

FIG. 5. Histograms of discriminant scores for male buntings. Scores for the reference specimens are plotted on the upper diagram, (A), and various combinations of the specimens from the Great Plains on the lower diagrams: (B) all 101 of the Great Plains males; (C) only the males taken 10 km S Chadron, 1969; (D) the males taken along

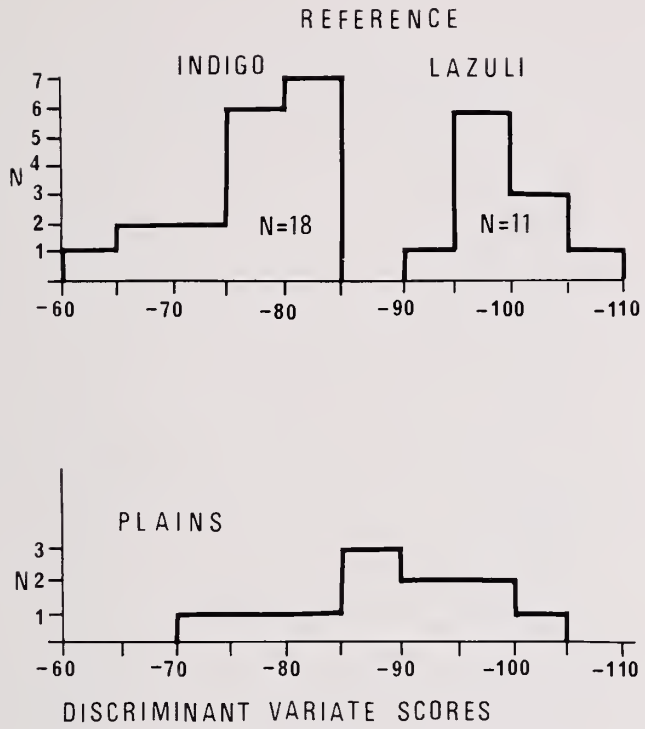

FIG. 6. Histograms of discriminant scores for female buntings. Scores for the reference specimens are plotted on the upper diagram, and those for the females from the Great Plains on the lower. The statistical lower extreme for Lazuli females is –89.6; the statistical upper value for Indigo females is –87.5.

The 19 Lazuli Buntings in Wyoming and Colorado sang a total of 51 song figure types, 40 of which had precise counterparts in the song catalog for Lazuli Buntings recorded from farther west. Thus, in areas of allopatry, there was little tendency for the song figures of either species to deviate from more eastern or western populations or to converge upon intermediate characteristics.

At Chadron, within the zone of sympatry, the situation was different. Males with *P. amoena* plumage sang songs whose composition varied from 100%

←

Little Bordeaux Creek, 10 km ESE Chadron (1955, open; 1969, shaded); (E) males taken from the Valentine region in 1955; (F) and males taken from Valentine in 1969. The upper Indigo and lower Lazuli extremes are indicated by the dashed line. The letters inside the histograms indicate the location of certain specimens identified in Fig. 3.

Table 1

Percentage of *P. cyanea* and *P. amoena* Figure Types in Songs of Birds of Various Plumages near Chadron, Nebraska

P. cyanea plumage	% *cyanea* figure types
CU 34250	100
CU 34252	65
not collected	20
CU 34264	14
Intermediate plumage	
CU 34257	100
CU 34247	9
P. amoena plumage	% *amoena* figure types
CU 34249	100
CU 34254	100
CU 34260	100
CU 34243	100
not collected	100
not collected	89
not collected	88
CU 34256	87
CU 34248	80
not collected	64
not collected	55
not collected	44
CU 34259	0
CU 34245	0

Lazuli figure types to 100% Indigo types (complete song interchange). Similarly, different individuals in *P. cyanea* plumage sang songs containing varying numbers of Indigo and Lazuli figure types. Table 1 shows the song composition of all males recorded at Chadron in terms of Indigo and Lazuli figures. One bird intermediate in plumage characteristics (CU 34257) sang a song composed entirely of Indigo figures, whereas a second intermediate male (CU 34247) sang a primarily Lazuli song. Three figures not found in other Lazuli Bunting populations were sung by males in *amoena* plumage at Chadron. Figure 7 shows examples of song composition of birds of different plumage types.

Even in this zone of sympatry no intermediate song figures were discovered. Intermediacy between the species' songs did occur, but it was achieved

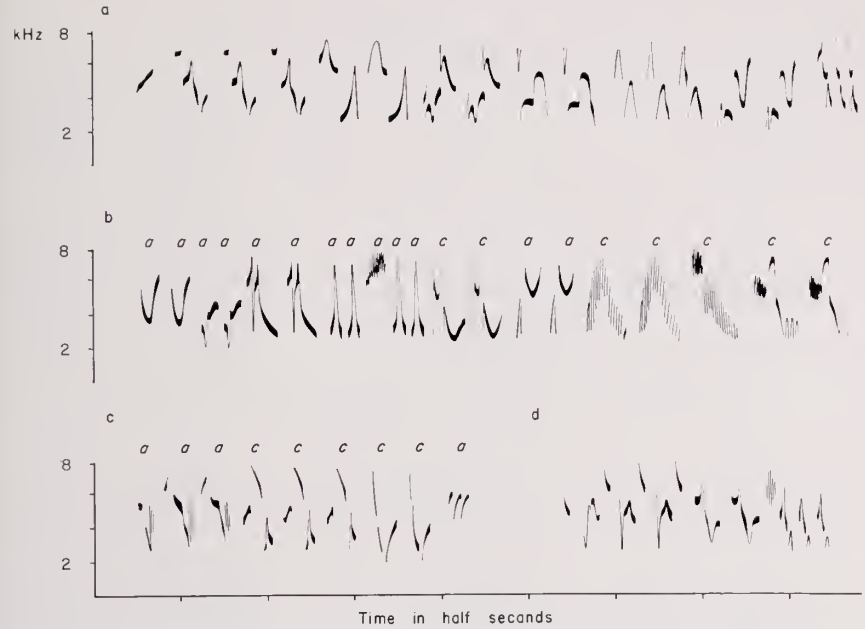

FIG. 7. Songs of some male buntings at Chadron, Nebraska. (a) Male in *P. cyanea* plumage (CU 34250) singing 100% *P. cyanea* song figures. (b) Male in *P. cyanea* plumage (CU 34252) singing both *P. cyanea* and *P. amoena* figures. Letters above figures indicate those from *cyanea* and *amoena* catalogs. (c) Male in *P. amoena* plumage (CU 34261) singing a mixture of *P. cyanea* and *P. amoena* figures. (d) Male in *P. amoena* plumage singing all *amoena* figures.

by an individual bird incorporating both pure *amoena* and pure *cyanea* figures into its territorial song.

Repetition index.—One feature of the songs of both species is the marked tendency for song figures to be repeated in pairs or even triplets (Thompson 1968, Emlen 1972). Table 2 presents the repetition index values obtained during our transect across the Plains. When these Plains data are lumped into "eastern," "western," and "Chadron" (sympatry) categories, no significant differences are apparent ($\chi^2 = 2.85$). Closer examination of all the data, however, suggests a possible trend toward increased degree of repetition in the Plains.

Frequency of buzzes.—We defined a "buzz" as a song figure that contained a series of rapid frequency reversals. The ninth figure in song b of Fig. 7 is a good example.

Efforts to compare songs with respect to their "buzziness" are complicated by the fact that *P. cyanea* songs tend to be longer than *P. amoena* and also

Table 2

Repetition Indices for *Passerina* Songs Recorded at Different Locations

Species	Locality	Number of birds	Repetition index
P. cyanea	Eastern United States	62	1.77*
P. cyanea	Eastern Nebraska (allopatric zone)	31	1.86
All birds pooled	Chadron, Nebraska (sympatric zone)	21	2.10
P. amoena	Western Wyoming and central Colorado (allopatric zone)	17	2.00
P. amoena	Western United States and southwestern Canada	30	1.95

* Pooled mean from Thompson's (1968) studies in Michigan and Emlen's (1972) studies in New York.

that the data were not normally distributed. We calculated the ratios of buzzes to non-buzzes and analyzed by chi-square tests. When the eastern and western samples are pooled and compared with the birds at Chadron there is a significant difference ($\chi^2 = 7.63$, $p < 0.05$) with the birds at Chadron showing a greater frequency of buzzes. No tendency for differential buzziness among the 3 phenetic categories at Chadron was distinguishable ($\chi^2 = 2.49$, $p > 0.05$).

Temporal features of song.—The spacing between successive song figures is somewhat different in Indigo and Lazuli buntings. The Indigo has a slower cadence to its song with a mean inter-figure interval of 0.09 sec. There is a further temporal subdivision of song structure with the interval between successive repetitions of similar figures being regularly and significantly shorter than the interval between dissimilar figures ($p < 0.001$: factorial analysis of variance). This temporal organization is one of the most regular features of *P. cyanea* song (see Table 3, Emlen 1972).

Among Lazuli Buntings, the song cadence is significantly quicker with mean intervals between successive song figures of 0.05 sec (Thompson 1968). The differences in the intervals between identical and dissimilar figures are not significant in this species.

Along our transect, the recorded songs of Indigo Buntings from areas east of the Chadron sympatry zone were similar to their far eastern counterparts; similarly, the Lazuli Bunting songs from Colorado and Wyoming were basically similar to Lazuli songs from the far west (see Table 3).

TABLE 3

TEMPORAL FEATURES OF *PASSERINA* SONG

Locality	Number of birds	Number of intervals analyzed	Mean interval (sec) between successive song figures			Standard error
			Dissimilar	/	Similar	
Eastern U. S. (Michigan & New York)	86		0.09		0.07	
Eastern Plains						
(Iowa and eastern Nebraska)	30	173	0.09			0.0026
		171			0.07	0.0018
Chadron, Nebraska						
(all morphs pooled*)	20	124	0.07			0.0020
		136			0.05	0.0018
Chadron Indigo morph	(4)			(0.069)		
Chadron intermediate morph	(2)			(0.056)		
Chadron Lazuli morph	(14)			(0.054)		
Western Plains						
(Colorado & Wyoming)	20	94	0.06			0.0022
		100			0.05	0.0017
Western United States						
(California, Utah & British Columbia)	23		0.05		0.05	

* Morphs described here are determined on the basis of plumage only.

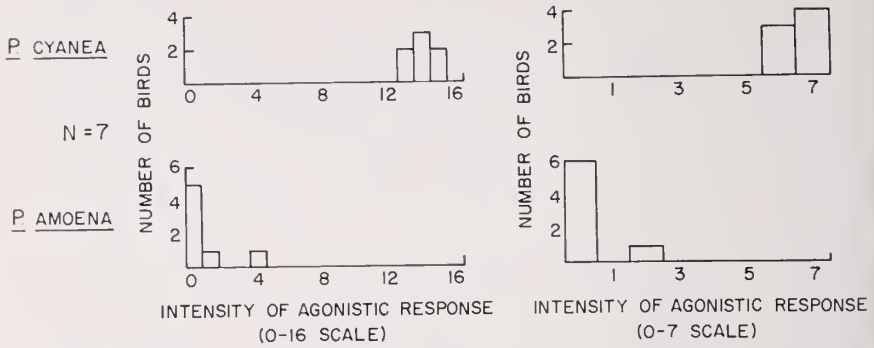

FIG. 8. Agonistic responses of territorial male Indigo Buntings at Niobrara, Nebraska, to playback of songs of Indigo Bunting (top) and Lazuli Bunting (bottom) song. Left: Responses measured on a 0–16 "Character Index" scale. Right: Responses measured on a 0–7 "maximum intensity" scale. Test songs used are those shown in Fig. 2.

At Chadron the temporal characteristics of song were intermediate. The mean intervals between similar and dissimilar successive song figures were 0.05 and 0.07 sec respectively. This trend toward intermediacy was due primarily to a shift toward faster cadence among *P. cyanea*. Although several individual *P. amoena* showed weak tendencies toward intermediacy, most did not and the mean values for temporal intervals were not statistically different from those of Lazuli Buntings recorded farther to the west. Hence the trend toward convergence was shown primarily by individuals of the less common species.

Behavioral Interactions

Niobrara, Nebraska.—We performed playback experiments to 7 territorial males here, all Indigo Buntings which had little, if any, contact with phenetic Lazuli Buntings. Each gave an intense agonistic response to the *P. cyanea* test song, but essentially ignored the *P. amoena* test song (Fig. 8). Only one bird (CU 34222) showed any interest in the Lazuli song, answering the playback with "long songs" and giving an occasional "chip" call (mild alarm). It ceased responding, however, and flew off while the test was still in progress.

These results are basically similar to ones obtained previously in areas of allopatry. Thompson (1969) found that *P. amoena* songs elicited only weak, if any, responses from male *P. cyanea* in southern Michigan although one Lazuli Bunting song was more stimulatory than were others. In New York, territorial Indigo Buntings showed no response when presented with the same Lazuli Bunting song shown in Fig. 2 (see Fig. 10 in Emlen 1972).

Valentine, Nebraska.—We recorded the songs of 18 birds, performed play-

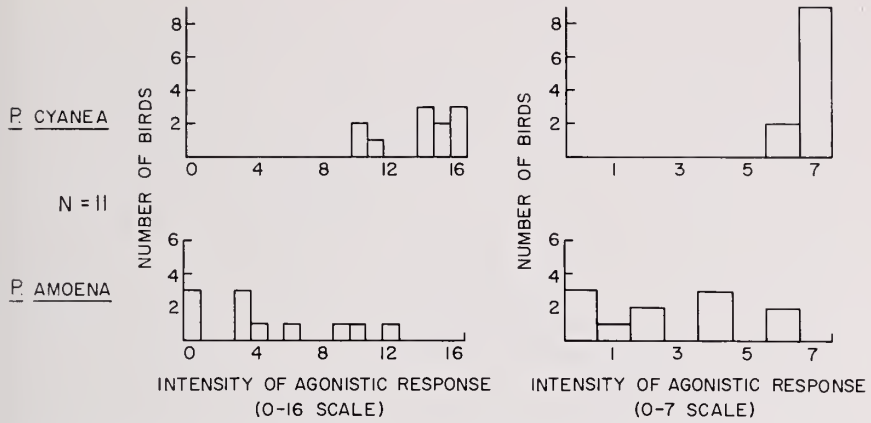

FIG. 9. Agonistic responses of territorial male *P. cyanea* at Valentine, Nebraska, to playback of songs of Indigo Bunting (top) and Lazuli Bunting (bottom).

back experiments to 11, and collected 18 specimens here. All were "pure" Indigo Buntings. Each individual gave a strong agonistic response to the *P. cyanea* test song (Fig. 9). Unlike the birds near Niobrara, these gave mixed responses to the *P. amoena* song. Three birds (CU 34229, 34237, 34238) showed no sign of song recognition, failing even to break their normal singing pattern when the playback was presented. Four others (CU 34224, 34227, 34228; 1 not collected) gave mild responses, ranging from increasing their rate of singing, to giving "alarm calls" and displays, to approaching the speaker and making display flights over it. The remaining 4 birds (CU 34225, 34226, 34235, 34236) showed strong responses involving numerous display flights, calls, modified singing behavior, and actual attacks on the speaker. In no instance, however, was a bird's response to the Lazuli Bunting song so strong as it was to the Indigo song.

We interpret these findings to imply that some of the Valentine birds have had previous experience with Lazuli song types and have learned to recognize and to respond to *P. amoena* song as that of a competitor. Interestingly, they retained this responsiveness even though no phenetic *P. amoena* were seen or heard near Valentine.

Chadron, Nebraska.—Ten km south of Chadron, Nebraska, we encountered and collected buntings of both species plus a small number of intermediate individuals. We performed playback experiments to 10 territorial males and found that every bird, regardless of phenotype, gave a full agonistic response to *both* song types (Fig. 10). We next tested whether the birds responded any more strongly to one song type over the other. All birds (regardless of

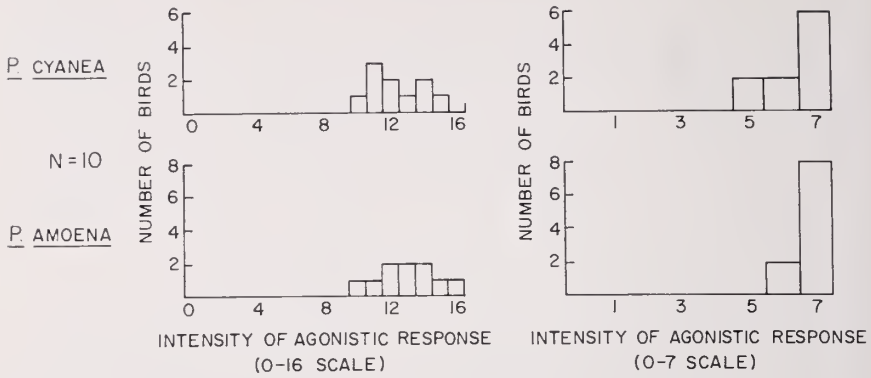

FIG. 10. Agonistic responses of territorial male buntings (both species plus intermediates) from Chadron, Nebraska, to playback of songs of *P. cyanea* (top) and *P. amoena* (bottom). See Table 4.

phenotype) were pooled in this test but the hypothesis of significant differences in response was rejected ($p > .1$. Wilcoxon Sign-Rank Test). A second hypothesis states that birds of a particular phenotype should respond most strongly to the playback of the song appropriate to that phenotype (i.e., *amoena* phenotype to *amoena* song). No such tendency to respond more strongly to "conspecific" song was observed and this hypothesis also was rejected ($p > 0.1$).

In the last section, we reported that birds at Chadron frequently sang songs including varying numbers of "pure" song figures from both *Passerina* species. In some instances a bird sang a song consisting entirely or primarily of heterospecific song figures. If we arbitrarily categorize individuals whose songs contain 25–75% figures of the heterospecific type as "intermediate" and those with greater than 75% "inappropriate" figures as examples of "song interchange," we can ask whether birds respond more strongly, not to their own plumage type, but to their own song type. This hypothesis is also rejected ($p > .1$), indicating that buntings at Chadron respond equally to either song.

Other observations of the birds at Chadron nicely complement the results of the playback experiments. The density of buntings was high and they were in the peak of breeding with males singing vigorously and defending territorial boundaries. These borders were defended equally against both species with the result that suitable habitat was subdivided into a series of non-overlapping, interspecific territories. Figure 11 depicts the territory locations at one study site 10 km S Chadron. Of 8 birds mapped, 6 were collected representing 3 "pure" Lazuli Buntings (CU 34254, 34256, and 34259, occupying territories F, G, and J on the map), 1 "pure" Indigo Bunting (CU 34252,

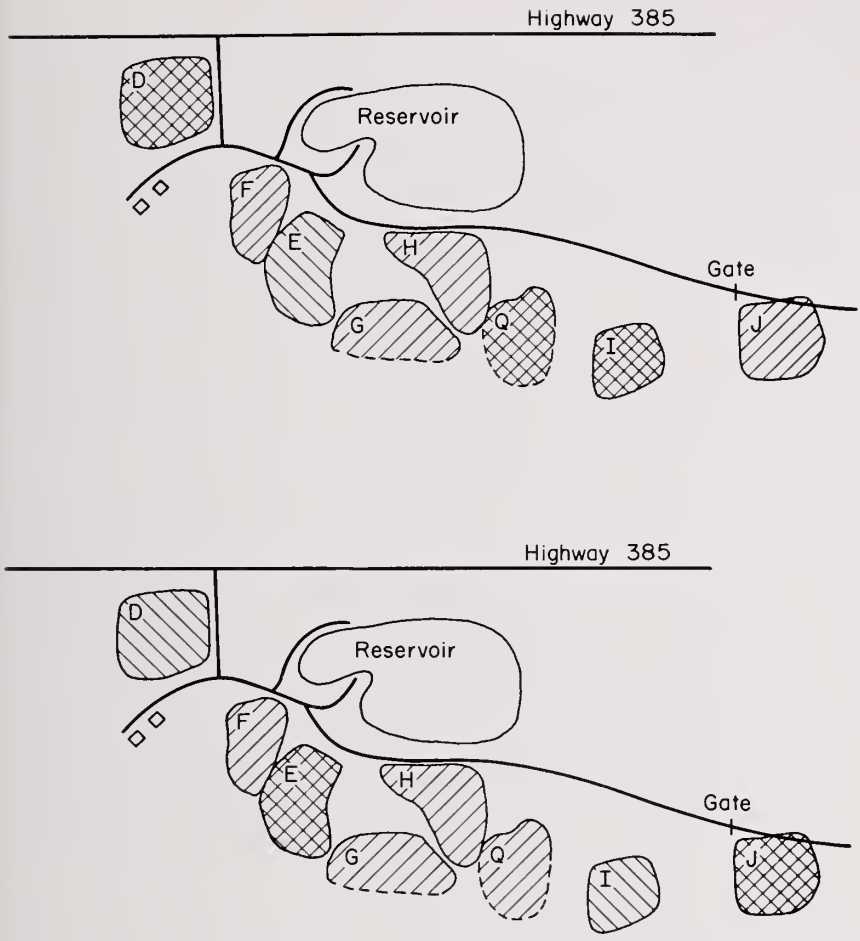

FIG. 11. Map of territorial boundaries of *P. cyanea*, *P. amoena*, and intermediates from 10 km S Chadron, Nebraska. Top: Territory owners identified on the basis of plumage. Bottom: Territory holders identified on the basis of their song. (See text).

occupying territory E), and 2 intermediates (CU 34251 and 34257; territories D and I). Two additional birds were observed but not collected; these were tentatively identified by plumage characters as being another Lazuli Bunting (on territory H), and an intermediate (territory Q). Several of

these birds sang either heterospecific (as defined above on the basis of figure types) or intermediate songs. Thus E appeared to be *P. cyanea* yet sang an intermediate song, whereas J appeared to be *P. amoena*, but had a 100% *P. cyanea* song. The 2 known phenetic intermediates both sang predominately Indigo-like songs, whereas the presumed intermediate (on territory Q) had a Lazuli-like song. Figure 11, which maps these territories in terms both of phenotype and of song type, shows the mosaic assortment of interspecific territories.

Border encounters involving aerial chases, displays, or in one instance, prolonged combat, were observed between 8 "pairs" of territorial males (Table 4). Two cases involved 2 "pure" Lazuli Buntings in which both visual and acoustical cues could be considered "conspecifically appropriate." Five encounters featured rivals with inappropriate or intermediate visual cues but appropriate song types. The remaining instance was a "pure" Lazuli–"pure" Indigo encounter in which neither visual nor auditory stimuli were conspecifically appropriate. This latter was the most intense aggressive interaction any of us have witnessed among *Passerina*. Bird CU 34250 intruded into 34249's territory and was routinely chased back. However, 34250 turned back (presumably near the territory border) and engaged 34249 in actual physical combat. The 2 birds met breast-to-breast and appeared to grapple with the legs while remaining almost stationary in the air. After a brief period they tumbled to the ground and remained there a meter or so apart. They then resumed the conflict, took to the air and leg-grappled while they hovered or slightly ascended. This was repeated 4 times before the birds separated, each returning to its own territory. Table 4 reveals that border encounters were most frequently observed between neighbors with "appropriate" songs, regardless of visual phenotype. The overall mosaic pattern of interspecific territories, however, and the aggressive fight described above attest that Chadron territorial males are able to recognize and respond to other buntings irrespective of plumage or song characteristics.

Similar isolated instances of interspecific territorial behavior between Indigo and Lazuli buntings have been reported from Utah by Wells (1958) and Whitmore (in press).

We made a special attempt to record male-female behavior, to locate nests, and to collect females at the study areas near Chadron. We succeeded in collecting the mates of 5 males and made visual identifications of 2 others (Table 5). All proved to be phenotypically *P. amoena*. (The visual assessments of the uncollected birds were based on the presence of white wing bars and the lack of striped breast appearance.)

The male members of the pairs include 5 *P. amoena*, 1 *P. cyanea*, and 1

TABLE 4

MORPHOLOGICAL AND SONG CHARACTERISTICS OF MALE *PASSERINA* OBSERVED IN TERRITORIAL BORDER ENCOUNTERS AT CHADRON, NEBRASKA

Male 1			Male 2			Appropriateness of cues	
Bird	Morph type	Song type	Bird	Morph type	Song type	Acoustical	Visual
CU 34248	a[1]	a	CU 34249	a	a	+	+
Not collected (H)[2]	a[3]	a[4]	CU 34256 (G)	a	a	+	+
Not collected (H)	a[3]	a[4]	Not collected (Q)	a–c[3,5]	a[4]	+	±
CU 34261	a	c[4]	CU 34262	c	c[4]	+	—
CU 34264	c	a	Not collected (M)	a[3]	a[4]	+	—
CU 34264	c	a	Not collected (O)	a[3]	a[4]	+	—
CU 34254 (F)	a	a	CU 34252 (E)	c	a–c[3,5] (65% a)	±	—
CU 34249	a	a	CU 34250	c	c	—	—

[1] a = *amoena*, c = *cyanea*.
[2] Letters in parentheses refer to territory locations in Fig. 11.
[3] Identification based on plumage alone.
[4] Song based on field notes alone (song not tape recorded).
[5] a–c = intermediate.

intermediate. Birds CU 34252 and 34253 are a mixed pair: examination of the female revealed the presence of large follicles suggesting that she was egg-laying or in early incubation. The pair CU 34257–34258 is also of interest: the male is intermediate in plumage and by PCA while his mate is a typical *P. amoena*. Our behavioral notes and ovary examination show this pair also to be in the early egg-laying stage.

Song playback experiments test the abilities of *males* to discriminate between conspecific and heterospecific songs. But they reveal nothing about *female* responsiveness. Since female discrimination and preference could be crucial for species segregation. it is informative to examine the data in Table 5 more closely. The sample sizes are small, but of the 7 Lazuli females, 5 were mated with males that were also visually Lazuli Buntings. When the males are partitioned on the basis of song types, only 3 females were mated

TABLE 5

COMPOSITION OF MATED PAIRS FROM CHADRON, NEBRASKA, WITH NOTES ON THEIR NESTING BEHAVIOR

Male				Female		
Identification	Age	Morph type	Song type	Identification	Morph type	Stage of breeding cycle
CU 34254	Adult[1]	a[2]	a	CU 34255	a	4 advanced fledglings
CU 34256	Adult	a	a	Not collected	a[3]	Advanced nestlings (female seen several times with food)
Not collected		a[3]	a[4]	Not collected	a[3]	Unknown
CU 34261	Adult	a	c[4]	CU 34263	a	Advanced nestlings plus 1 cowbird egg (nestlings collected)
CU 34259	Adult	a	c	CU 34260	a	2 advanced young (almost ready to fledge)
CU 34252	Adult	c	a–c[5] (65% a)	CU 34253	a	Early incubation (ovary with large follicles)
CU 34257	Adult	a–c[5]	c	CU 34258	a	Nest building or egg-laying (ovary with enlarging follicles)

[1] Second year or older.
[2] a = *amoena*, c = *cyanea*.
[3] Identification based on plumage alone.
[4] Song based on field notes alone.
[5] a–c = intermediate.

to *P. amoena* types, the remaining males having intermediate or predominately *P. cyanea* songs.

If we assume that individuals expressing "appropriate" behavioral signals for mate selection spend less time in pair formation and courtship, we would predict that such pairs would be at a more advanced stage in the breeding cycle than pairs consisting of birds possessing less optimal or inappropriate stimuli. Table 5 shows that 4 pairs had advanced nestlings or fledged young; in each case the male was of the appropriate visual phenotype while in only 2 of the 4 instances did the male sing a "conspecific" song. The remaining 2 pairs were in the early incubation or egg-laying stages. In one, the male sang an intermediate song, but was of the opposite visual phenotype: in the other, the male was of intermediate plumage and sang a heterospecific song.

Admittedly any statement drawn from these small samples must be regarded as speculative, but the data suggest that female Lazuli Buntings may rely more heavily on visual than upon acoustical cues in mate selection, at least in zones of sympatry.

Little Bordeaux Creek, Nebraska.—We spent only one afternoon at Little Bordeaux Creek, 10 km ESE of Chadron, but several findings lead us to believe that Little Bordeaux Creek was fundamentally different from the other Chadron study area and might have been a less optimal, overflow, area for *Passerina*. We observed 5 male and 2 female buntings, collecting 3 males and both females.

All 3 males collected were 1st-year birds whereas all 12 males collected from 10 km S Chadron were in their second breeding season, or older.

Although no quantitative playback experiments were performed here, both Indigo and Lazuli songs were played in attempts to lure birds in for collecting. The buntings seemed to respond, but frequently 2 or more males would be called in. This resulted in numerous chases, and we surmised that either territorial boundaries had not yet stabilized, or non-territorial (presumably unmated) males were present.

Finally, both females collected were in early stages of reproduction. One had not yet developed an incubation patch and had a granular ovary; the other had an incubation patch but had not yet laid (largest follicle = 4 mm). On the basis of this small sample, pair formation and breeding seemed retarded compared with the other Chadron study sites.

These findings, coupled with our subjective impression of sub-optimal bunting habitat along the Little Bordeaux, lead us to speculate that this sample might represent individuals that were unable to establish territories or obtain mates in other areas. In this regard, it is especially interesting that a high percentage of the birds collected here showed signs of intermediate morphology. One of the females (CU 34246) was "misidentified" by DFA, 2 of the males (34242, 34243) were outside the reference clusters on DFA (Figs. 5 and 6), and the third male (34245) may be intermediate by PCA (Fig. 3; bird "O"). The remaining female (34244) seemed intermediate by plumage, yet clustered with *P. amoena* in both DFA and PCA.

Shoshoni, Wyoming.—Glendo, Wyoming is west of any area of sympatry found by Sibley and Short. We had expected this to be our final study site and although we located several apparent Lazuli Buntings here, the first bird we called in with playback was an obvious intermediate which, though not collected, appeared similar to CU 34257, and had a short, *P. cyanea*-sounding song.

Consequently, our study ended north of Shoshoni where we did find an

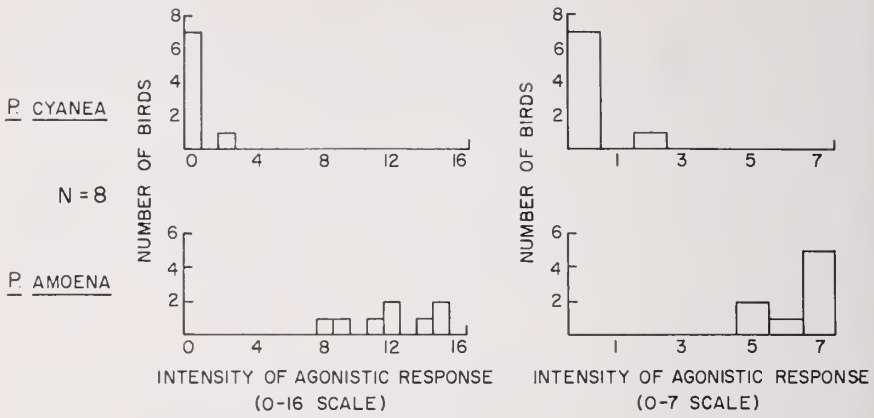

FIG. 12. Agonistic responses of territorial male Lazuli Buntings at Shoshoni, Wyoming, to playback of *P. cyanea* (top) and *P. amoena* (bottom) songs.

allopatric population of Lazuli Buntings. The 6 males collected here were phenetically *P. amoena* as were the 11 songs recorded. We performed playback experiments to 8 males whose territories were strung out almost linearly along a narrow creek bed. The results provide an exact converse to the Indigo Buntings from Niobrara: each male responded strongly to playback of the *P. amoena* song, but failed to respond to *P. cyanea* song (Fig. 12).

In summary, birds of both species from populations outside the zone of possible sympatry clearly distinguish between Indigo and Lazuli songs and respond only to that of the conspecific. Within areas of contact, song response parameters are broadened to encompass both song types and either will elicit the full repertoire of agonistic behaviors.

DISCUSSION

Morphological Variation

All of our data from PCA, DFA, and simple visual assessment of plumage suggest the same conclusions: (1) Individuals intermediate in size and plumage between Indigo and Lazuli buntings occur in the Plains. (2) These are restricted to a few areas where both "typical" species also occur and thus are presumed to be hybrids. (3) These hybrids are uncommon, comprising only 6 or 7% of the specimens. (4) There is no evidence to suggest introgression. All but the few specimens from the Plains mentioned in this paper fall within the range of variation of eastern and western stocks. This additionally suggests that geographic variation in size within Lazuli and Indigo buntings must be slight, although they differ from each other. (5) The

Indigo Bunting appears to be extending its range westward at the expense of the Lazuli Bunting. Both the change in species composition at Chadron and Valentine between 1955 and the present study, and the occurrence of intermediate forms and *P. cyanea* song influence as far west as Glendo, Wyoming suggest this.

The lack of correspondence between the individuals intermediate in size and color (and song, for that matter) is interesting. Inasmuch as a small percent of the reference specimens for DFA are "misidentified," it is conceivable that intermediates identified by this program are inappropriately so characterized. However, the fact that 5 of the 6 male hybrids identified by DFA are from the zone of distributional overlap in Nebraska (4 are from Little Bordeaux Creek: 1 is from Valentine, 1955), and the sixth is an extralimital specimen of a "Lazuli" taken from southwestern Kansas, where Indigo Buntings occur regularly in low density (Rising 1974), leaves random error an unlikely and uncompelling explanation. Rather, this suggests independent assortment between mensural and color features. In short the number of birds identified as intermediate by any analysis stressing any one correlated set of features is low, but only specimens from sympatric populations were found to be intermediate by any of our criteria.

Song Variation

Buntings from the eastern and western edges of the Plains sang songs that were indistinguishable from reference song types recorded in Michigan and New York (Indigo) or Texas and California (Lazuli). But in the zone of sympatry several song modifications were evident: (1) The tendency to repeat song figures in pairs, triplets, or more was highest at Chadron. (2) Figures with a "buzzy" quality were more prevalent at Chadron. We have no adequate explanation for these trends but raise the possibility the "buzziness," as well as repetition of song figures, might somehow be adaptive for transmission of information in the dry, windy, Plains environment. (3) The cadence of Indigo song is significantly slower than Lazuli, as a result of a longer average interval between successive song figures. At Chadron, the mean values for inter-figure spacings were intermediate between typical eastern (Indigo) and western (Lazuli) values primarily as a result of cadence shifts among Indigo Buntings. (4) The individual song figures recorded from birds at Chadron were no different from those sung by buntings elsewhere in North America. Almost every figure had a structural counterpart in the catalogs of *Passerina* song figures drawn from allopatric populations of either *P. cyanea* or *P. amoena*. The remarkable finding is that an individual male would include in its song, figures from *either* or *both* the Indigo and the Lazuli catalogs, singing them "perfectly" regardless of his morpho-

logical phenotype. The percentage of "appropriate" figures varied between individuals, ranging from 100% correct to cases of complete song interchange.

We found no evidence for vocal character displacement in the area of sympatry. Rather, 2 song features showed an increased frequency in both species (repetition index and occurrence of buzzes) whereas 2 other features appeared to be "intermediate" between the parental songs (intervals between figures and actual figure types). Interestingly, "intermediacy" was shown in precisely those parameters experimentally demonstrated to be of extreme importance for male-male recognition in a previous study by Emlen (1972). Our results thus are consistent with Cody's (1969) hypothesis that among species that derive significant benefit from interspecific territoriality, selection will favor convergence of auditory and/or visual stimuli that promote interspecific recognition. This convergence has the effect of facilitating heterospecific spacing. Such convergence is far from complete in the buntings and "intermediacy" of song figures refers to intermediate percentages of *P. cyanea* and *P. amoena* figures, not to intermediate figure structure. Furthermore, figure shape and temporal spacing can be dissociated so that many birds of both species sang *P. cyanea* figures, but sang them with something like *P. amoena* spacing.

Interspecific Territoriality and Responsiveness to Heterospecific Song

Both Indigo and Lazuli buntings from populations outside the area of sympatry clearly distinguished between conspecific and heterospecific song and responded only to the former. At Chadron, in the area of overlap, all birds apparently failed to discriminate between the test songs: they maintained mutually exclusive interspecific territories and responded aggressively to intrusion by any other bunting, regardless of its plumage or song type. At Valentine, just east of the present zone of contact, the birds (all *P. cyanea*) gave mixed responses to *P. amoena* song. Some individuals discriminated between the songs; others gave mild to strong responses to the heterospecific song.

We propose that an individual bunting's behavior, upon hearing a heterospecific song, is determined by its prior behavioral experience with birds of the opposite species or song type. For example, if a bunting interacted with another bird of conspecific plumage but which sang an intermediate or heterospecific song, it could come to associate a wide range of song types with conspecific competitors and would respond accordingly in future encounters. A similar, although converse, experience could lead to the recognition of and defense against the heterospecific or intermediate plumage type.

In areas of sympatry, such interactions between birds of different plumage types or song types presumably are quite common. In fact, at Chadron, only

33% of the males proved to be both visually and (appropriately) vocally "pure." But how could Indigo Buntings from Valentine have had contact or interacted with Lazuli Buntings? We suggest 2 possibilities. First, some *P. amoena* might have been present in the area but not located by us. The habitat becomes more xeric farther away from the river and Lazulis frequently inhabit more arid habitats than Indigos (Wauer 1969); hence a few *P. amoena* may have been in these areas. Also, Sibley and Short (1959) found evidence of Lazuli Buntings at Valentine in 1955. Thus some of our Indigo Buntings may have encountered Lazulis earlier in the breeding season, prior to settling on a permanent territory.

The common tendency for 1st-year passerine birds to settle and breed some distance from their natal site (Nice 1937, Lack 1946) suggests a second explanation for the heterogeneous responses of the Valentine birds. Those individuals showing strong recognition of Lazuli Bunting song may represent birds reared in areas farther to the west where Indigo–Lazuli interactions are more frequent. This tendency for 1st-year *P. cyanea* to wander has been documented in Michigan by Thompson (1972), who found colormarked adult buntings returning to his study area over a 4 to 5 year period, but did not recover any birds marked as nestlings or fledglings.

Not all the birds that reacted to Lazuli Bunting song were second year males, however. Of four 1-year-old birds tested, 2 (CU 34236, 34226) responded, one of them giving the strongest Valentine response to *P. amoena* song. Unless these birds had encountered Lazuli Buntings at Valentine during their brief period of mobility prior to territory establishment, we must assume that they learned to recognize Lazuli Bunting song the previous year—during the summer and autumn of their hatching. If true, this would imply that song recognition occurs at a time prior to the development of singing behavior or to the initiation of territorial or aggressive responses to song.

Both Rice and Thompson (1968) and Emlen (unpublished observations) believe that the critical period for song learning in *P. cyanea* occurs not in the summer and autumn of hatching, but in the following spring. This raises the intriguing possibility of the existence of 2 separate processes in the ontogeny of bunting song: one associated with learning song *utterances* and another with song *recognition.*

Gill and Murray (1972) have suggested a similar behavioral model (based on a bird's individual experience) to explain a very different pattern of responsiveness to interspecific song in the genus *Vermivora.* Blue-winged (*V. pinus*) and Golden-winged warblers (*V. chrysoptera*) from allopatric populations frequently fail to distinguish between their Type I songs. But in southern Michigan, in an area of sympatry, Gill and Murray found that

discrimination was improved: Blue-wings ceased responding to heterospecific songs. They hypothesized that the 2 species' songs were extremely similar and interspecific responses were the result of misidentification. But where one species encounters the other, individuals have the opportunity to associate in appropriate plumage cues with heterospecific song. These individuals should then become more discriminating, limiting their responsiveness to song types associated with birds of conspecific plumage.

The 2 species of *Vermivora* are morphologically distinct and Gill and Murray (1972) found no evidence of direct ecological competition or of interspecific territoriality.

We did not collect any information concerning the degree of ecological separation between Indigo and Lazuli buntings. Rather, we assume that the presence of strongly defended, interspecific territories implies either that ecological divergence is minimal or that divergence normally present in other parts of their ranges cannot be expressed within the restricted bands of riparian habitat available along the rivers crossing the Plains.

Murray (1971) suggested that interspecific territoriality is usually maladaptive and results from one or both species misidentifying or failing to discriminate the other. Although "misidentification" occurs among male buntings at the zone of sympatry, we believe that this "misidentification" is adaptive in promoting the establishment and maintenance of interspecific territories. In effect, we hypothesize that sympatric buntings "learn" to misidentify congeners as a result of individual behavioral experiences. This argument is based on the assumption that the extra energy expended in defending a territory against heterospecific or intermediate phenotypes is less than the energy that would be lost through the mutual sharing of territories.

For forms that are extremely similar ecologically, or which may not have had sufficient opportunity to diverge ecologically (for a variety of possible reasons), a responsiveness to both Indigo and Lazuli song clearly would be adaptive in promoting interspecific territoriality and thus minimizing ecological competition or interference. The tendency for the songs of such birds to show "convergence" in precisely those song parameters known to play a role in male–male recognition would further enhance heterospecific identification by minimizing the information loss inherent in using a conspecific song in interspecific communication.

If females are unable to discriminate between Indigo and Lazuli song types, this could lead to increased hybridization at the zones of sympatry. This possibly is one explanation for the hybrid birds and mixed pairs we observed. The relative rarity of these mis-matchings, however, suggests that females additionally use other cues in the mate selection process.

TABLE 6

FREQUENCY OF MALE TYPES IN THE POPULATION 10 KM S CHADRON COMPARED TO THE TYPES MATED TO *P. AMOENA* FEMALES

	Plumage types		
	amoena	*cyanea*	intermediate
Frequency in male population:	64% (14/22)	23% (5/22)	13% (3/22)
Frequency of mated males:	71% (5/7)	14% (1/7)	14% (1/7)
	Singing types		
	amoena	*cyanea*	intermediate
Frequency in male population:	60% (12/20)	20% (4/20)	20% (4/20)
Frequency of mated males:	43% (3/7)	43% (3/7)	14% (1/7)

Pair Formation and the Success of Intermediates

Studies of behavior of females and of the success of mixed pairs are crucial to an understanding of the present and future interactions of *Passerina* in the Plains. In regions where only one species occurs regularly, behavioral selection may well be against an immigrant individual that exhibits an "odd" plumage or song. Thus, there may be effective segregation of the species in regions where one is uncommon. But what occurs in areas where both forms are common? How accurate is the female–male recognition and what are the consequences of "inappropriate" pairing?

Unfortunately, our samples are too small to perform statistical tests to answer the first question. At Chadron (excluding Little Bordeaux Creek), 64% of the males in the population were morphologically *P. amoena* as compared with 71% of those males mated to *P. amoena* females (Table 6). Alternatively, 60% of the male population sang *P. amoena* song types (defined on the basis of $> 75\%$ appropriate song figures) as compared with 43% of the males mated to *P. amoena* females (Table 6). Females thus are pairing with the appropriate visual phenotype slightly more often, and with the appropriate singing type less often, than would be expected on the basis of a purely random selection of mates.

Data from several indirect sources suggest that mixed pairs and hybrids may be at a selective disadvantage. First, hybrid individuals are uncommon. Second, our analyses revealed practically no evidence of introgression. Third, our behavioral and ecological notes from the Little Bordeaux Creek area suggest that this is a sub-optimal area, populated by 1st-year male buntings that are considerably retarded in territory development and breeding behavior.

Four of the 5 birds collected there proved to be intermediate by either PCA or DFA and the fifth seemed intermediate in plumage. Finally, both the mis-matched pair and the hybrid pair from Chadron were delayed in their breeding when compared to the 4 "pure" pairings.

If mixed pairings are disadvantageous, natural selection should favor accurate female–male selection. Data in Tables 5 and 6 suggest that females at Chadron may rely more heavily on visual than upon auditory information in selecting mates. If true, this would be advantageous since in *Passerina*, morphology is a better indicator of genotype than song and there can be no selection for accurate female–male selection unless the cues used have a genetic basis. Details of song are learned and, where both species are in close contact, cases of intermediate song and song interchange are frequent.

For use in territorial advertisement, however, song is the more nearly optimal cue. Acoustical advertisement carries over greater distances and penetrates through concealing vegetation, thus freeing the male from having to physically patrol his territory, making his visual appearance known to would-be intruders. Song also enables a male to indicate his awareness of an intruder and to issue a mild threat, without actually flying to the location of the intrusion. In many instances, this is sufficient to repel the trespasser. Such subtle use of acoustical information can result in considerable energetic savings. The equal responsiveness of both species to both song types at Chadron, and the tendency toward intermediacy in some song features support the view that song is a principal advertisement cue for male–male interactions among these sympatric populations of *Passerina*.

Evolutionary Status of Passerina *in the Plains*

The ranges of Indigo and Lazuli buntings in the Plains seem to be in a dynamic state. In Nebraska the Indigo Bunting has apparently displaced the Lazuli Bunting westward, perhaps as much as 215 km in 15 years (1955–1969). Interestingly, a comparable modification of range may have been made by the eastern and northern Baltimore Oriole (*Icterus galbula*) at the expense of its geographic complement, Bullock's Oriole (*I. galbula*) in the northern Plains (Rising 1973). The east-facing and west-facing ranges of *P. amoena* and *P. cyanea* may well be "sharpened" by the presence of the congener. An "odd bird" will rarely find a mate. Nevertheless, the combination of variables that variously gives the adaptive edge to either *P. amoena* or *P. cyanea* probably shifts subtly, and the changes in the ranges of the birds are sequelae of these changes. If we assume that adult buntings return to previous breeding sites with high fidelity, this rapid change in range suggests that first-year dispersal distances of these birds must be large. This would have some

important implications: stochastic phenomena, such as the random fixation of a song- or morph-type, are unlikely. An abrupt or limited zone of sympatry thus would appear to be stable and dynamically maintained by natural selection (Endler 1973).

Thus, the evolution of the *Passerina* in the Great Plains need not be in a transitional stage. If hybrid individuals have reduced fitness, as would seem to be the case, it is probable that genetic divergence between the forms has progressed beyond the point of probable return. Genetic convergence in the future, therefore, seems unlikely.

SUMMARY

In the summer of 1969 we studied the morphology and behavior of the Indigo Bunting (*P. cyanea*) and the Lazuli Bunting (*P. amoena*) along a transect across the Great Plains. We concentrated on studying singing, territoriality, and mating behavior of known individuals that were later collected for morphological examination. Our hope was that this integrative approach would lead to a better understanding of the breeding biology of *Passerina* at their zone of contact.

An examination of 274 specimens showed that most individuals from the Plains fall within the normal ranges of eastern (*P. cyanea*) or western (*P. amoena*) reference populations as defined by either principal components analysis or discriminant functions analysis. Only 6 to 7% of the specimens showed signs of intermediacy (hybridization) and there was little evidence of introgression.

Intermediate specimens as well as both phenotypes were encountered near Chadron, Nebraska. Comparisons of the species compositions collected by us and by Sibley and Short (1959) indicate a rapid westward shift in the range of *P. cyanea* and, correspondingly, in the location of the area of sympatry.

In areas of allopatry in the Plains, the songs recorded from *Passerina* were indistinguishable from those of their counterparts recorded far to the east or west. At Chadron, however, birds of both species sang songs incorporating figures from both song types. For example, *P. amoena* songs ranged from 100% "appropriate" (100% *P. amoena* figures), through intermediates, to cases of complete song interchange (100% *P. cyanea* figures). Temporal parameters of song also tended to converge toward intermediate values at Chadron, especially among the less common species (*P. cyanea*).

Behavioral playback experiments showed that territorial male *P. cyanea* from the eastern Plains (Niobrara) respond agonistically only to songs of conspecifics; *P. amoena* songs are ignored. Conversely, *P. amoena* from the western Plains (Shoshoni) respond fully to playback of *P. amoena* song but fail to recognize the song of the congener. At Chadron, however, both species as well as intermediates give full agonistic responses to *either* song type. We hypothesize that buntings learn to respond to heterospecific song as a result of individual encounters and experiences.

Territorial behavior observed at Chadron complemented these findings. The birds were interspecifically territorial, with both species as well as intermediates defending territorial boundaries against all other *Passerina*.

An analysis of mated pairs at Chadron suggested that most females were mated to appropriate males and that inappropriate pairings (defined morphologically) were delayed in their breeding compared to normal pairings. We speculate that females rely, at least

in part, on visual cues in mate selection; such a strategy clearly would be advantageous since morphology is a good predictor of genotype whereas song (which is learned and often "inappropriate" at Chadron) is not.

Four lines of evidence suggest that mis-matings, where they occur, are selectively disadvantageous: (1) the small number of intermediate individuals and minimal introgression found, (2) the rarity of mixed-mated pairs, (3) the temporal retardation of breeding of such pairs, and (4) the occurrence of a high percentage of both first-year males and intermediate phenotypes at one particular study site that was judged on the basis of vegetation to be sub-optimal.

We conclude: (1) That massive convergence and introgression is not occurring among the *Passerina* of the Great Plains. (2) The species appear to have diverged to a point where hybrids and mixed-pairs are at a selective disadvantage. (3) The 2 forms minimize possible ecological competition through the maintenance of non-overlapping, interspecific territories. Both the changes in singing behavior and the increased responsiveness to congeneric song noted in the area of sympatry are seen as adaptations that promote recognition of, and aid in the defense of, these territories against heterospecifics.

ACKNOWLEDGMENTS

This work was supported in part by an NIH health science advancement award to S. T. Emlen and Cornell University. The manuscript has profited from comments and criticisms by N. J. Demong, D. Forsythe, D. Hussel, J. C. Rice, T. L. Rising, S. A. Rohwer, R. C. Rybczynski, V. H. Schaefer, and F. W. Schueler. Computing was carried out at the Univ. of Toronto Computing Center. We are especially grateful to W. C. Dilger for painting the frontispiece and to the George M. Sutton fund for financing its reproduction.

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DIVISION OF BIOLOGICAL SCIENCES, SECTION OF NEUROBIOLOGY AND BEHAVIOR, CORNELL UNIV., ITHACA, NY 14853; DEPT. OF ZOOLOGY, UNIV. OF TORONTO, AND THE ROYAL ONTARIO MUSEUM, TORONTO, CANADA M5S 1A1; AND DEPT. OF BIOLOGY, WAYNE STATE UNIV., DETROIT, MI 48202. ACCEPTED 28 JUNE 1974.

Appendix 1

Character Index Scores for Male *Passerina*

Region	Index score	Description
Head	0	forehead cobalt blue, as in *cyanea*
	1	forehead intermediate
	2	forehead turquoise blue, as in *amoena*
Rump	0	cobalt, as in *cyanea*
	1	turquoise, as in *amoena*
Wing bars	0	absent, as in *cyanea*
	1	reduced
	2	present, middle covert ca. 5 mm white, as in *amoena*
Abdomen	0	cobalt, as in *cyanea*, or with a few white feathers
	1	mottled
	2	white, or light buffy-brown, as in *amoena*
Breast band	0	cobalt, as in *cyanea*
	1	mixed (rusty and blue, or white and blue)
	2	bright rusty, as in *amoena*
Throat	0	cobalt, as in *cyanea*
	1	intermediate
	2	turquoise, as in *amoena*

Appendix 2

Character Index Scores for Female *Passerina*

Region	Index score	Description
Throat and breast	0	throat whitish; breast light gray-brown, and conspicuously but faintly streaked; breast rarely with blue, as in *cyanea*
	1	light tawny or cinnamon brown; breast unstreaked or only faintly so, as in *amoena*
Wing bars	0	lesser secondary coverts indigo bluish; middle coverts edged with light buffy brown; greater faintly buffy edged, as in *cyanea*
	1	lesser coverts light blue-green; middle coverts edged with pale white or cinnamon; greater coverts buffy brown, as in *amoena*
Back and rump	0	generally unicolored, olive-brown, faintly streaked; rump can be bluish, as in *cyanea*
	1	back light brown, with faint streaks; rump grayish-blue and unstreaked, as in *amoena*

Appendix 3

Character Projections Computed for Principal Components Analysis

Sex	Character	Projections	
		Component 1	Component 2
Male	Crown Color	0.3544	0.0706
	Back "	0.3556	0.0534
	Breast "	0.3553	0.0760
	Belly "	0.3529	0.0661
	Rump "	0.3357	0.0685
	Under Tail Covert Color	0.3544	0.0714
	Wing Length	0.3057	–0.2651
	Tail "	0.3031	–0.2224
	Tarsus "	0.0501	–0.6408
	Culmen "	–0.2663	–0.1733
	" Width	0.0129	–0.6417
Female	Throat Color	0.4489	–0.0688
	Wing Bar Color	0.4380	–0.0101
	Back Color	0.4315	–0.0944
	Wing Length	0.4020	0.2664
	Tail "	0.4172	0.1677
	Tarsus "	0.0594	0.6653
	Culmen "	–0.2812	0.4112
	" Width	–0.0474	0.5248

Appendix 4

Discriminant Weights Computed for the 5 Characters Measured on Male and Female *Passerina*

Sex	Character	Discriminant weight
Male	Wing Length	–1.522007
	Tail "	–1.477634
	Tarsus "	4.058525
	Culmen "	6.514037
	Culmen Width	–1.201126
Female	Wing Length	–2.315963
	Tail "	–1.868002
	Tarsus "	8.098619
	Culmen "	6.085967
	Culmen Width	–1.173168

WEIGHTS AND WING LENGTHS OF WILD SONORAN MASKED BOBWHITES DURING FALL AND WINTER

Roy E. Tomlinson

Bobwhite (*Colinus virginianus*) populations extend from Minnesota south to the Mexican state of Chiapas (approximately 3500 km) and from the far eastern United States west to central Colorado (approximately 2800 km) (Aldrich and Duvall 1955). The species has a complex and definable pattern of morphological variation which is clinal throughout most of its range (Aldrich 1946). The Masked Bobwhite (*C. v. ridgwayi*), a geographically isolated form, inhabits mesquite-grasslands at elevations of 120–730 m in the state of Sonora, Mexico. This population once extended into southern Arizona but was extirpated there by overgrazing of suitable habitat before 1900 (Tomlinson 1973a). Its current status in Sonora is critical as a result of continued land abuse, and the bird has been listed as "endangered" since 1966 (Bureau of Sport Fisheries and Wildlife 1966, 1968, 1973). I conducted an ecological study of this endangered population during 1968–72 (Tomlinson 1973b), and efforts to reestablish the Masked Bobwhite in the historical range of Arizona are currently underway (Tomlinson 1973c).

This paper presents weight and wing measurement information obtained from wild-captured Sonoran birds, compares weights with those of other Bobwhite populations in the U.S. and Mexico, and discusses Bergmann's Rule as it pertains to the Bobwhite.

METHODS

During the three fall-winter seasons between 1968 and 1971, 187 Masked Bobwhites were captured near Benjamin Hill, Sonora as part of a life history study (Table 1). At the time of capture, I examined each bird and recorded sex and age, stage of primary molt, wing length, and total body weight. A standard U.S. Fish and Wildlife Service band was attached to one leg.

Weights were obtained in the field on a 500-g Hanson Dietetic scale, accurate to 1 g. A special millimeter board was used to measure one wing of each bird from the bend of the wing to the tip of the longest primary when the primaries were fully extended. Wing lengths obtained by this method are known to be slightly longer and therefore not directly comparable with standard museum wing (chord) measurements (Aldrich 1946—103–111 mm chord length for 7 specimens of Masked Bobwhite vs. 107–120 mm for 52 adult specimens in this study). Molt category was determined by noting the most recent primary to fall, but measurements of emerging primaries were not attempted; exact aging of immatures (Petrides and Nestler 1952) was therefore not possible and approximate figures are used for comparative purposes. I distinguished adults from immatures by differences in coloration of primary coverts (Leopold 1939, Haugen 1957). Separation of subadults from older adults was not practicable during the trapping periods because most birds had molted through their eighth and ninth primaries and distinguishing char-

TABLE 1

SUMMARY OF MASKED BOBWHITE TRAPPING NEAR BENJAMIN HILL, SONORA, MEXICO, WINTERS 1968–1970

Fate of Trapped Birds	Adults		Immatures			Total
	Male	Female	Male	Female	Unknown	
Saved for propagation stock	10	8	16	23	0	57
Banded and released	18	10	25	15	1	69
Recaptured and released	8	2	25	13	2	50
Died in traps	1	4	1	5	0	11
Total	37	24	67	56	3	187

acteristics were usually lacking. Accordingly, subadults were grouped with adults. Weights of recaptured adults (repeats) were not included in the summaries of adult weight data (Table 2) to avoid introducing biases in the small sample. Data from recaptured immatures, however, were included in the summaries of weights of immatures (Table 3), as weight gains between trappings represented new information.

RESULTS

Adult Weights and Wing Lengths—The average weight for 26 adult males was 168.6 g, and for 19 adult females, 162.8 g. Weights for males generally followed a normal frequency distribution, but those for females tended to be clustered at both ends of the distribution. Examination of the data by month revealed that the lowest weights for females were generally obtained in October. Pooled t-tests (Dixon and Massey 1951:103) indicated that October females (156.3 g) were significantly lighter than females caught later (168.7 g) ($t = 2.25$, $P < 0.05$, 17 d.f.), that male weights were not significantly different between October (166.1 g) and later samples (170.8 g) ($t = 1.59$, $P > 0.10$, 24 d.f.), and that there were no significant differences between all males (168.6 g) and those females caught after October (168.7 g) ($t = 0.03$, $P > 0.10$, 34 d.f.). Females probably reach their lowest annual weight in October because this population nests later than U.S. Bobwhite populations and sometimes does not bring off broods until late October or early November (Tomlinson 1973b:305). After October, average weights for the sexes are not significantly different (170.7 g for males and 168.7 g for females; $t = 0.47$, $P > 0.10$, 22 d.f.). This conclusion was also reached for Bobwhites in the Midwest (Hamilton 1957, Roseberry and Klimstra 1971).

Average wing length for 31 adult males was 113.5 mm, and for 21 adult females, 112.9 mm (Table 2). Mean wing lengths for each sex were not significantly different ($t = 0.88$, $P > 0.10$, 50 d.f.), although females again tended to have more individuals at each extreme of the frequency distribution.

Table 2

Average Weight (g) and Wing Length (mm) by Month of Adult Wild Sonoran Masked Bobwhites

	WEIGHT			
	MEAN		RANGE	
Month	Male	Female	Male	Female
Oct.	166.1(12)[1]	156.3(9)	149–179	147–170
Nov.	173.8(5)	175.0(3)	165–181	157–195
Dec.	167.0(6)	167.0(3)	162–173	146–179
Jan.	173.0(3)	165.2(4)	173–173	150–176
Overall	168.6(26)	162.8(19)	149–181	146–195
± t.05 S.E	± 3.04	± 6.10		

	WING LENGTH			
	MEAN		RANGE	
Month	Male	Female	Male	Female
Aug.	111.5(2)	–	110–113	–
Oct.	113.2(14)	112.5(11)	110–117	110–116
Nov.	115.8(5)	115.3(3)	115–118	112–120
Dec.	113.4(7)	114.6(3)	112–115	110–117
Jan.	112.8(3)	110.5(4)	111–114	107–112
Overall	113.5(31)	112.9(21)	110–118	107–120
± t.05 S.E.	± 0.72	± 1.28		

[1] Sample size in parentheses—Discrepancies in sample sizes from Table 1 due to summer trapping and/or measurement of dead birds. No trap repeats included.

Immature Weights and Wing Lengths—Immature weights and wing lengths (Table 3) were grouped according to the stage of their primary wing molt rather than by month as with adults. This grouping allows comparison of young birds at various ages. The actual ages of these birds are unknown although an estimate can be made if one assumes that Masked Bobwhites molt at the same rate as their midwestern counterparts (Petrides and Nestler 1952). Birds molting the second primary could not be accurately sexed because of incomplete plumage development.

Weights of immature Masked Bobwhites increased from about 75 to 158.0 g for females and to 169.9 g for males between their second and eighth primary molt stages, for an average weight gain of approximately 85 to 95 g in about 3 months. Simultaneously, the average wing length of Masked Bobwhites increased from 98 to 112.6 mm for females and to 112.2 mm for males. This growth rate compares well with that of immature Illinois birds, which gained from 78 to 174 g during the same physiological period (Roseberry and

TABLE 3

AVERAGE WEIGHT (G) AND WING LENGTH (MM) BY PRIMARY MOLT CATEGORY FOR IMMATURE SONORAN MASKED BOBWHITES[1]

Primary Molt Category	Approx. Age in Days	WEIGHT MEAN Male	WEIGHT MEAN Female	WEIGHT RANGE Male	WEIGHT RANGE Female
2	37	75.0 (2)[2]		75–75[2]	
4	50	91.0 (3)	88.5 (2)	78–100	81–96
5	65	126.7 (3)	132.0 (3)	114–136	130–134
6	80	140.1 (14)	128.3 (6)	122–158	118–137
7	99	160.3 (28)	146.9 (33)	138–192	124–172
8	126	169.9 (9)	158.9 (8)	159–180	146–179

Primary Molt Category	Approx. Age in Days	WING LENGTH MEAN Male	WING LENGTH MEAN Female	WING LENGTH RANGE Male	WING LENGTH RANGE Female
2	37	98.0 (2)[2]		97–99[2]	
4	50	103.0 (2)	102.0 (2)	103–103	102–102
5	65	111.0 (7)	109.0 (3)	108–114	105–111
6	80	109.0 (9)	107.5 (4)	107–110	106–109
7	99	111.8 (27)	110.1 (35)	107–117	105–115
8	126	112.2 (9)	112.6 (8)	110–115	110–114

[1] Sample size in parentheses. Samples include trap repeats for both weight and wing length and dead birds for wing length.

[2] Incomplete plumage development for these two birds did not allow accurate judgement of sex.

Klimstra 1971). Wing length data from the Midwest are not available for comparison.

Young Masked Bobwhites had essentially reached adult size and weight by the time they molted their eighth primaries. The older immature males averaged slightly heavier than adult males (169.9–168.6 g, $t = 0.45$, $P > 0.10$, 33 d.f.) but had slightly shorter wings (112.2–113.5 mm, $t = 1.74$, $P > 0.05$, 38 d.f.). Immature females weighed less than adult females (158.9–162.8 g, $t = 0.76$, $P > 0.10$, 25 d.f.) and had completed growth of wing feathers (112.6–112.9 mm, $t = 0.28$, $P > 0.10$, 27 d.f.). Although not statistically significant in this study, a relatively lighter weight of immature females in comparison to other age and sex classes was also observed in the Illinois study.

DISCUSSION

Weight data for certain Bobwhite populations in the U.S. have been presented by several authors. Hamilton (1957) gave an excellent review of

Bobwhite winter weights in relation to geographical location in the U.S. Roseberry and Klimstra (1971) presented voluminous weight data for Bobwhites taken in southern Illinois during all seasons of the year. These authors, as well as Ripley (1960) and Robel and Linderman (1966), discussed Bergmann's Rule as it pertains to this species, i.e., that body size, and therefore weight, increases from south to north in the U.S. A positive correlation between latitude and weight was observed by each writer.

Bergmann's ecogeographical rule was defined by Mayr (1963) as follows: "Races from cooler climates tend to be larger in species of warm-blooded vertebrates than races of the same species living in warmer climates." James (1970) and McNab (1971) recently reviewed this rule as applied to birds and mammals, respectively. McNab (1971) concluded that mammals generally do not follow the rule. James (1970), however, presented strong evidence that, "Intraspecific size variation in homeotherms [12 species of birds] is related to a combination of climatic variables that includes temperature and moisture." And that, "Small size is associated with hot, humid conditions, larger size with cooler or drier conditions." She further describes the clinal aspects of size changes in relation to topography and latitude.

A modification of Hamilton's (1957) summary, with additional data on Bobwhite populations from Mexico provided by Leopold (1959) and by my study, is presented in Table 4. These data suggest that the varied populations in Mexico also increase in weight from south to north. The correlation coefficient for the mean weights and respective latitudes in Table 4 is 0.95. The discrepancies (in Morelos and the uplands of south-central Mexico) possibly occur because the birds were collected at higher elevations and this factor probably affects weight as does latitude (James 1970:375 and 387–388).

The area in Sonora where the Masked Bobwhites were trapped during my study is almost exactly at 30°N latitude, which corresponds to north Florida and southern Georgia where Stoddard (1931) reported an average weight of 165 g for all age and sex Eastern Bobwhites encountered during the fall and winter. I obtained an almost identical figure (165.7 g) when weights for all immatures in the eighth primary molt category and all adults were averaged. Thus, weights of Bobwhites, at the same latitude but of different populations and separated by over 2600 km longitudinally, are astonishingly alike. James (1970) found that the bird species she examined tended to be larger in dry climates than in moist climates with approximately equal average temperatures. Although Sonora has a drier climate than Florida, the high temperature and humidity during the July–September rainy season in Sonora (the breeding season of the Masked Bobwhite, Tomlinson 1973b) may be the selective force affecting weights similar to those of the Florida population.

Bergmann's Rule, as defined by Mayr (1963), appears to hold true for

TABLE 4

AVERAGE WEIGHTS OF BOBWHITES DURING FALL AND WINTER AS RELATED TO LATITUDE (MODIFIED FROM HAMILTON 1957 AND LEOPOLD 1959)

Location of Study	Approx. Latitude, °N	Average Wt. (g)	N	Authority
Chiapas, Mexico	16	129	?	Leopold (1959)
Morelos, Mexico	19	149	?	"
Vera Cruz, San Luis Potosi, Mexico (coastal)	21	133	?	"
San Luis Potosi, Jalisco, Queretaro, Mexico (uplands)	22	159	?	"
Tamaulipas, Nuevo Leon, Mexico	24	152	?	"
Florida	25–30	161.6	?	Nelson and Martin (1953)
Sonora, Mexico	30	165.7	65	Tomlinson (this study)
N. Florida and S. Georgia	30–31	165.0	188	Stoddard (1931)
South Carolina	32	176.3	244	Stoddard (1931)
S. Illinois	37	178.2	847	Roseberry and Klimstra (1971)
S. Missouri	37	186.0	166	Leopold (1945)
Central Missouri	39	176.3	215	Hamilton (1957)
Leetonia, Ohio	41	186.8	108	Stewart (1937)
Dunn Co., Wisconsin	45	203.0	845	Buss, et al. (1947)

Bobwhites from Chiapas, Mexico, to the northern distributional limits of the species in the U.S. Hamilton's (1957) suggestion that the quality of soils at different latitudes might be the causative factor for weight differences in Bobwhites has some merit but it should be pointed out that soil quality also varies greatly from place to place at the same latitude. The explanation that the birds' weights have become adjusted through the evolutionary process to more easily regulate body temperature in relation to air temperature and humidity (James 1970) seems to be more plausible.

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FERTILITY OF EGGS PRODUCED ON TERRITORIES OF VASECTOMIZED RED-WINGED BLACKBIRDS

Olin E. Bray, James J. Kennelly, and Joseph L. Guarino

One approach toward reducing populations of Red-winged Blackbirds (*Agelaius phoeniceus*), and thus the agricultural damage that they cause, is through a program of interfering with their ability to reproduce (Davis 1961), such as with a chemosterilant. Such a program in Red-wings might be best directed toward the male, because the species is polygynous (Allen 1914) and territorial males normally maintain a harem of 1 to 4 females. However, incidents of promiscuity have been reported in females (Allen 1914, Beer and Tibbitts 1950), and as a result of this or other factors, chemosterilization of only some fraction of the males in a local population might not result in a proportional reduction in fertile clutches. To explore the effects of a sterilized-male program, we conducted studies with breeding Red-wings in small marshes near Lakewood, Jefferson Co., Colorado, in 1971 and 1972. To circumvent the problems inherent in the development of an effective chemosterilant and to insure that each treated male was sterile, we surgically sterilized territorial males by vasectomy. The relative numbers of infertile and fertile clutches produced on territories of these males are presented here, along with discussions of their possible implications.

METHODS

Vasectomy study, 1971.—As techniques were still being developed, no formal sampling design was used in selecting the location or number of males that were vasectomized in the 2 cattail (*Typha* sp.) marshes studied (Red-wings were also present in other nearby habitats). From 19 to 26 May (after nesting had started), 8 territorial male Red-wings were captured, anesthetized with Metofane (Pitman-Moore, Inc., Fort Washington, Pa.), and bilaterally vasectomized. (Reference to trade names does not imply U.S. Government endorsement of commercial products.) To expose each vas deferens, a small incision was made on each side of the cloaca just anterior to the seminal sac. The distal segment of each vas deferens was ligated with 5-0 chromic cat gut about 3 to 5 mm from its entrance into the cloaca, and the segment between the ligature and cloaca was cut. After the incisions were closed, the birds were banded with both a U.S. Fish and Wildlife Service and a colored aluminum band. Then the birds were placed within their territories where they recovered rapidly and without any apparent ill effects.

We collected eggs from nests in the territories of vasectomized males to determine fertility and encourage renesting. As nesting had started before the males were vasectomized, their females could have been carrying viable sperm. Therefore, clutches started before vasectomy were not collected until 9 days after the operation; this allowed a period of approximately ¾ of the incubation period for retained sperm to lose viability before

females were induced to renest. Clutches started after vasectomy were collected about 2 days after the last egg was laid; Red-wing females lay one egg a day and start incubating the day the last egg is laid (Beer and Tibbitts 1950, Payne 1969). This reduced the chance of predation and allowed time for a greater number of renests.

Collected clutches were artificially incubated in a Jamesway Model 252 incubator. Eggs that did not hatch were opened and were considered infertile if no development was evident. Clutches were considered fertile if any of the eggs were fertile. Fertility was also determined for eggs in 45 clutches from territories of 10 normal males. These were incubated either naturally or artificially.

Sperm retention by females.—We could not locate references to the length of time that females of passerine species retain viable sperm, so in 1971 we arbitrarily chose a 9-day waiting period before collecting eggs to induce renesting. To investigate the sperm retention period of Red-wings, in 1971 we shot or trapped 30 females nesting outside the study marshes and examined the reproductive tracts for sperm. Females were obtained at 7 reproductive stages: nest-building; the day the second egg was laid; the first, sixth, and eleventh days after incubation started; and the sixteenth and twenty-first days after incubation started (females with young). We checked 17 females for sperm soon after they were shot or trapped (group I), and 13 females were held in captivity for 10 days before being examined (group II). The reproductive tract of each female was removed in toto and flushed with physiological saline; the flushings were then checked for motile sperm. As sperm are trapped in crypts in the infundibular and uterovaginal glands of some birds (Bobr et al. 1964), each tract was then tied at both ends and filled with saline until it was turgid; these flushings were then checked for sperm. Each tract was then fixed in Bouin's fluid, histological sections were prepared, and the relative abundance of sperm in each histological section was estimated.

Vasectomy study, 1972.—Due to the fertile clutches that occurred on territories of males vasectomized in 1971, studies were conducted in 1972 to determine the effects of sterilizing different proportions of territorial males in different marshes.

To minimize the influence of territorial males outside the study marshes, these tests were conducted in 4 of the most isolated small cattail marshes. Marsh I was a control marsh; all 6 males there were sham-operated (they underwent surgery, but the vas deferens was neither ligated nor cut). All 3 males in marsh II were vasectomized, but the site served as a test area with only 30% of the males sterilized; this was because 7 normal territorial males were present within .3 km of the marsh, in a wet pasture and an alfalfa (*Medicago sativa*) field. In marsh III, 4 of the 8 males were vasectomized; the territories of the sterilized birds were grouped together. In marsh IV, all 8 males were vasectomized.

We operated on the males between 9 May (start of nesting) and 22 May. Anesthetic techniques were the same as in 1971, but surgical techniques differed in that 2 ligatures about 2 mm apart were tied around the most distal part of each vas deferens and the intervening segment was severed. After the incisions were closed, each male was marked with a colored aluminum leg band and 5×2.5 cm plastic leg streamer attached with a U.S. Fish and Wildlife Service band (Guarino 1968); the birds were then placed within their territories to recover.

Because of the results of the 1971 sperm retention tests, all clutches were left in the nests until the eleventh day of incubation; this was about the start of hatching. Clutches or broods were then destroyed to induce the females to renest. Fertility of clutches was determined by candling (Evans 1951) 2 or 3 days after the last egg was laid. Candling detected fertility in some eggs of some clutches on the day after the last egg was laid;

TABLE 1

FERTILITY OF CLUTCHES ON TERRITORIES OF 6 MALE RED-WINGS VASECTOMIZED IN 1971

Days after vasectomy	No. of clutches	No. of fertile clutches	Percent of fertile clutches
1–4	9	9	100
5–11	2	0	0
12–18	13	9	69
19–25	11	8	73
26–32	6	5	83
33–39	6	4	67
40–46	1	1	100
	48	36	

the detection of fertility improved to include all eggs of some clutches on the second day after laying was completed and all eggs of all clutches on the third day. As an additional check, eggs that had not hatched by the eleventh day were opened and were considered infertile if no development was evident. Predators destroyed about 20 clutches on the study areas before the eggs were candled; thus, some fertility information was lost.

As in 1971, we did not detect any change in aggressiveness or behavior of vasectomized males. Near the end of the nesting season, 5 vasectomized and 3 untreated males were shot and the testes and vasa deferentia were examined grossly and then microscopically in histological sections. In comparison with untreated birds, the vasectomized birds had very small testes but large and distended vasa deferentia; some of the vasa deferentia contained a cheesy material. Sperm were present in the vasa deferentia proximal to the ligatures, but none were observed in the distal portions.

RESULTS

Vasectomy study, 1971.—Infertile clutches were found on the territories of 6 of the 8 vasectomized males. The 2 males with no infertile clutches had been vasectomized early in the study, and necropsies revealed sperm in the cloaca of each. These were the only 2 males that were not successfully vasectomized during the 2 years of study.

The shortest interval between vasectomy and the start of an infertile clutch was 5 days (Table 1). Thus, the fifth day after sterilization was considered the earliest that infertile clutches could have been started. Of 39 clutches started 5 days or more after vasectomy on the territories of the 6 successfully sterilized males, 27 (69%) were fertile. All eggs were fertile in 26 of the 27 fertile clutches, and all eggs were infertile in the 12 infertile clutches. The percentage of fertile clutches did not decrease with time after vasectomy (Table 1).

The proportion of fertile clutches on each territory ranged from 44 to 86% (4 of 9 to 6 of 7). The distance between territories of sterilized males and the

closest fertile male's territory varied from 27 to 137 m. Sterilized males with more isolated territories had lower percentages of fertile clutches than those with territories close to fertile males. We did not detect any change in aggressiveness or behavior of the vasectomized males, as compared to normal, untreated males.

Of the 45 clutches checked for fertility on territories of normal males, 43 (96%) were fertile. The 2 infertile clutches came from the territory of a male with one female, and it appears that one member of the pair was sterile.

Sperm retention by females.—Sperm were recovered in the saline flushings from only one female, a group I bird shot during nest-building. However, histological examination of reproductive tracts showed that most birds in both groups had sperm stored in the uterovaginal glands. The longest interval of sperm retention was by a group II female captured 16 days after incubation started. This female had 4 eggs, and if we assume that they were laid on consecutive mornings and that copulation ceased the day the third egg was laid (Beer and Tibbitts 1950, Payne 1969), she had retained sperm for about 26 days. However, the few sperm present were probably insufficient to fertilize a clutch.

The abundance of sperm observed in the uterovaginal glands appeared to be directly related to the stage of nesting. Sperm were abundant in the tracts of birds caught during nest-building or egg-laying, less abundant at the start of incubation, and few at hatching or shortly thereafter. It is not known if the sperm remaining in a female tract are capable of fertilizing eggs, but their presence indicates that it is possible. We therefore concluded that in future studies we should wait until the eggs were about ready to hatch before the clutches were collected to encourage females to renest.

Vasectomy study, 1972.—No infertile clutches were started less than 5 days after vasectomy. Thus, as in 1971, the fifth day after sterilization was considered the earliest that infertile clutches could have been started. The results of our candling of clutches, started 5 days or more after males were vasectomized or sham-operated, are summarized in Table 2. All clutches in marsh I (control marsh) were fertile, indicating that surgery did not stop copulation. In marshes II and III, 44 and 33%, respectively, of the clutches on territories of vasectomized birds were fertile. In marsh IV, 12% of the clutches were fertile.

At marsh II, one vasectomized male's territory was between those of the other 2 vasectomized birds, and his females had the lowest percentage of fertile clutches. At marsh III, fertile clutches were produced on only one vasectomized male's territory, which was between territories of both fertile and other vasectomized males. Thus, as in 1971, the most isolated males had the lowest percentage of fertile clutches.

TABLE 2

FERTILITY OF CLUTCHES STARTED 5 DAYS OR MORE AFTER SURGERY IN TERRITORIES OF VASECTOMIZED AND FERTILE RED-WINGS IN 1972

		Males		Clutches		
Marsh	Status	No.	Percent	No.	No. of fertile clutches	Percent
I	Fertile[a]	6	100	8	8	100
	Sterile	0	0	–	–	–
	Total	6		8	8	100
II	Fertile	7	70	11	11	100
	Sterile	3	30	9	4	44
	Total	10		20	15	75
III	Fertile	4	50	5	5	100
	Sterile	4	50	6	2	33
	Total	8		11	7	64
IV	Fertile	0	0	–	–	–
	Sterile	8	100	17	2	12
	Total	8		17	2	12

[a] Males were sham-operated (see Methods).

Only one egg was infertile in 8 clutches on territories of sham-operated males at marsh I, and only one was infertile in 16 clutches on territories of fertile males at marshes II and III. On territories of vasectomized males, all eggs were infertile in 24 clutches, and all eggs were fertile in 7 of 8 fertile clutches.

DISCUSSION

Fertile clutches.—As the vasectomized birds were apparently successfully sterilized, and we did not detect any change in their aggressiveness or behavior, the fertile clutches produced on territories of vasectomized males apparently were the result of sperm retention in the females from copulation before sterilization, replacement of females with new females carrying fertile sperm, or promiscuity by females. Given the choice of these explanations, we believe the fertile clutches may have been due to female promiscuity for the following reasons: the sperm retention study showed that few sperm were

retained after egg-laying was completed. the 1971 vasectomy study did not show a decrease in the percentage of fertile clutches with time after vasectomy (Table 1), and the most isolated males had the fewest fertile clutches.

All clutches on territories of fertile males near vasectomized birds were fertile. Thus, it appears that Red-wing females always copulate with their own males, as would be expected. but that they also copulate with other males—if the fertile clutches on territories of vasectomized males were indeed due to promiscuity.

The stage(s) in the nesting cycle when promiscuity occurs is unknown, as are the number and timing of copulations necessary to fertilize a clutch. Nero (1956) reported that Red-wings stop copulating before egg-laying begins, but R. B. Payne (pers. comm.) observed Red-wings copulating on approximately 10 occasions, and apparently all were during the female's egg-laying period. In our study, in 71 clutches laid 5 days or more after vasectomy on territories of vasectomized males in 1971 and 1972, 36 were completely infertile, 33 were completely fertile, and only 2 were partially fertile. If promiscuity occurred during egg-laying and contributed to fertilization of the clutch being laid, one would expect more partially fertile clutches than this. It is, of course, possible that some completely fertile clutches resulted from promiscuity throughout egg-laying, but it is hard to explain why steady promiscuity should occur at some times and no promiscuity at others. Perhaps copulation, including promiscuity, stopped before egg-laying began. We found no references indicating that passerine species do not require copulation during egg-laying to produce fertile eggs, but Lorenz (1959) obtained high egg fertility for 20 days after artificial insemination of Turkeys (*Meleagris gallopavo*). The infertile eggs in the 2 partially fertile clutches were probably not related to the territorial males being vasectomized. Occasional infertile eggs are not uncommon in the clutches of many species, and 2 of the 24 clutches on fertile males' territories also contained infertile eggs.

If fertile clutches on territories of vasectomized males were the result of promiscuity, the fact that the most isolated vasectomized males had the lowest percentages of fertile clutches suggests that females were promiscuous with nearby territorial males. However, some could have copulated with non-territorial adult males. Nero (1956) reported that territory-seeking Red-wing males commonly appeared on the breeding area throughout the breeding season. Orians (1961) and Holm (1973) obtained evidence that a non-breeding adult male population exists. The literature indicates that it is unlikely that females are promiscuous with one-year-old males, even though some are reproductively mature (Orians 1961, Payne 1969): Nero (1956) stated that female Red-wings usually are not receptive to one-year-old males.

and Wright and Wright (1944) said that one-year-old male Red-wings rarely copulate with females.

Factors Relevant to Male Chemosterilant Programs.—The effect of chemosterilants on Red-wings would probably vary by habitat type. In general, a larger proportion of fertile clutches should occur in habitats where there is more interchange among members of the population and more renesting. Holm (1973) reported that renesting was more likely in territories occupied by 3 or more females than in territories occupied by 1 or 2; and Case and Hewitt (1963), Dyer (1969), and our unpublished data have shown that Red-wing males in marshes tend to have more females than males in upland habitat. Jackson (1971) found that renesting was more common in marshes than in upland habitat. Upland nesters probably forage more within their own territories than marsh nesters (Jackson 1971), which would probably decrease the opportunity for promiscuity in upland areas. Thus, it appears that chemosterilants may be more effective on upland nesters than on marsh nesters.

It is possible that chemosterilants would somewhat reduce the number of young fledged per successful nest. Jackson (1971) found that clutches in renests had significantly fewer eggs than initial clutches. Thus, even if a female that originally bred with a sterile male did renest and breed with a fertile male, perhaps she would fledge fewer young than if her initial clutch had been fertile.

This study has shown that the number of fertile clutches produced on a Red-wing male's territory can be reduced by sterilizing the male, but that the extent of the reduction depends on the arrangement of neighboring fertile territorial males, and perhaps on the number of fertile nonterritorial males in the population. It appears likely that the results of chemosterilizing a certain proportion of the males in a marsh would be somewhat better than in our studies, where nests were systematically destroyed to encourage renesting. Studies with artificial eggs suggest that incubation of sterile eggs would be prolonged; Holcomb (1970) found that the incubation period of normal-sized artificial eggs averaged 19.4 days (range 1–26), and Jackson (1971) found that 3 female Red-wings incubated artificial eggs for 22–23 days. This would mean fewer renesting attempts, and thus fewer chances for a female who originally bred with a sterile male to encounter a fertile one.

SUMMARY

Six male Red-winged Blackbirds scattered throughout 2 marshes were vasectomized in 1971, and their females began laying infertile clutches in 5 days. However, of 39 clutches on their territories, 27 (69%) were fertile. In 1972, 30, 50, and 100% of the males in 3 small isolated marshes were vasectomized, and 44, 33, and 12% of the clutches on their territories were fertile, respectively. All clutches were fertile in a fourth marsh where

all males were sham-operated. All clutches checked were fertile on territories of fertile males adjacent to sterilized males. During the 2 years there were only 4 partially fertile clutches, 2 each on vasectomized and fertile males' territories.

Examination of reproductive tracts of female Red-wings from other marshes showed that sperm retained from copulation were abundant during nest-building or egg-laying but had dropped to a few by hatching.

In vasectomy studies, vasectomized males whose territories were the farthest from fertile males had the lowest percentage of fertile clutches. This and other evidence indicated that fertile clutches on territories of vasectomized males may have been due to females being promiscuous with fertile males.

The occurrence of fertile clutches on territories of vasectomized males indicates that sterilizing some of the males in a population (as in a chemosterilant program) would not result in a proportional decrease in fertile clutches. However, the decreases achieved (up to 88%), and the probability of better results in an actual program, indicate that male chemosterilization would be a feasible means of reducing Red-wing populations.

ACKNOWLEDGMENTS

We thank Brad E. Johns, Donald F. Mott, and Jerry D. Roberts of the Denver Wildlife Research Center for their help with laboratory and field work.

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NEW LIFE MEMBER

Dr. David E. Samuel is now a life member of the Wilson Ornithological Society. Dr. Samuel is an Associate Professor of Wildlife Biology in the Division of Forestry at West Virginia University. His principal interests in ornithology are with avian ecology and avian succession on strip-mined land. He has published a number of papers on Barn and Cliff swallows, and more recently he has been studying American Woodcock and Ruffed Grouse. In addition to his ornithological interests, Dr. Samuel enjoys hunting and fishing, backpacking, canoeing, and music.

FLOODPLAIN BIRDS OF WESTON BEND, MISSOURI RIVER

John L. Zimmerman and John L. Tatschl

The Weston Bend of the Missouri River lies 644 km upstream from St. Louis and is adjacent to Fort Leavenworth, Leavenworth Co., Kansas. Bird populations present on the floodplain at Fort Leavenworth were measured during 1973 and 1974 as part of a study of the terrestrial ecology of the Missouri River from Rulo, Nebraska to its mouth for the U.S. Army Corps of Engineers. This report summarizes the species diversities and densities recorded in summer and winter on census plots in pasture, cropland, oldfield, young forest, and mature hardwood forest. The oldfield, young forest and mature hardwood forest represent a typical successional series, while the cropland habitat, and to a lesser extent, the pasture, are common land uses in the floodplain of the river. Since the area is located on Fort Leavenworth, these seral habitats have been only moderately affected by cultural disturbances and provide a good example of the natural changes that occur in bird populations as a result of floodplain plant succession in eastern Kansas. Additionally, the area is of interest because it lies near the western fringe of the ranges of many bird species that are characteristic of the eastern deciduous forest.

METHODS AND DESCRIPTION OF THE VEGETATION

Trips were made to this site in the winter, summer, and fall from mid-February, 1973 to early January, 1974. Breeding bird populations in these 5 habitats were determined by marking the presence of territorial males on scale maps of the census areas on 31 May, 1–4 June, and 8–9 July, 1973. The number of visits to each habitat during this period varied with the difficulty in censusing; for example, 7 censuses were required in the mature hardwood forest, while only 3 were necessary in pasture and cropland. A preliminary reconnaissance was conducted on 17 February 1973, but winter populations were measured on the study plots during the period 7–9 January 1974 by walking transects through the habitats and recording the number of individuals of each species. In winter each habitat was censused twice.

The areas of the census plots are given in Table 1. All were relatively square except that in the mature hardwood forest, which was a long rectangle (152 m × 1100 m).

The species diversity index (H′) used is that of Shannon and Weaver (1949) and is given in units based on natural logarithms computed from the tables of Lloyd et al. (1968).

The mature hardwood forest has a canopy exceeding 20 m in height with hackberry (*Celtis occidentalis*) and elm (*Ulmus americana*) as dominant species. The understory is dominated by pawpaw (*Asimina triloba*), and coralberry (*Symphoricarpos orbiculatus*) is the most abundant shrub. Ground cover is largely tall nettle (*Urtica dioca*). Increment bores indicated that some trees in this stand were over 250 years old. The young forest is approximately 20 years old, and the co-dominants are pawpaw, cottonwood

Table 1

Breeding-bird Populations of the Leavenworth Floodplain

	Pasture		Cropland		Oldfield		Young forest		Mature hardwood forest	
Size in hectares	8.0		14.0		20.2		10.4		16.7	
Grasshopper Sparrow (*Ammodramus savannarum*)	(1)[1]	0.12[2]								
Dickcissel (*Spiza americana*)	(11.5)	1.44	(11)	0.79	(24.5)	1.22				
Red-winged Blackbird (*Agelaius phoeniceus*)	(7)	0.87	(2)	0.14	(32)	1.59				
Eastern Meadowlark (*Sturnella magna*)	(4)	0.50	(0.5)	0.04	(6.5)	0.32				
Western Meadowlark (*Sturnella neglecta*)			(0.5)	0.04						
Horned Lark (*Eremophila alpestris*)			(2)	0.14						
Common Yellowthroat (*Geothlypis trichas*)			(3)	0.21	(62)	3.08	(16)	1.54		
Bobwhite (*Colinus virginianus*)			(1)	0.07	(1)	0.05	(1)	0.10		
Indigo Bunting (*Passerina cyanea*)			(1)	0.07	(1.5)	0.07	(8)	0.77	(5)	0.30
Brown-headed Cowbird (*Molothrus ater*)			X[3]		X		X		X	

[1] territorial males observed
[2] males/ha
[3] cowbird densities not recorded

TABLE 1 (continued)

	Pasture	Cropland	Oldfield	Young forest	Mature hardwood forest
Short-billed Marsh Wren (*Cistothorus platensis*)			(2.5) 0.12		
American Woodcock (*Philohela minor*)			(1) 0.05		
American Goldfinch (*Spinus tristis*)			(1) 0.05	(3) 0.29	
Yellow-breasted Chat (*Icteria virens*)				(4) 0.39	
Gray Catbird (*Dumetella carolinensis*)				(1) 0.10	
Rose-breasted Grosbeak (*Pheucticus ludovicianus*)				(10) 0.96	(9) 0.54
Northern Oriole (*Icterus galbula*)				(9) 0.87	(8) 0.48
Rufous-sided Towhee (*Pipilo erythrophthalmus*)				(8) 0.77	(5) 0.30
Black-capped Chickadee (*Parus atricapillus*)				(5) 0.48	(6) 0.36
Common Flicker (*Colaptes auratus*)				(4) 0.39	(2) 0.12
Blue Jay (*Cyanocitta cristata*)				(4) 0.39	(4) 0.24
Yellow-billed Cuckoo (*Coccyzus americanus*)				(3) 0.29	(1) 0.06
Cardinal (*Cardinalis cardinalis*)				(3) 0.29	(10) 0.60

TABLE 1 (continued)

	Pasture	Cropland	Oldfield	Young forest		Mature hardwood forest	
Mourning Dove (*Zenaida macroura*)				(1)	0.10	(2)	0.12
Downy Woodpecker (*Dendrocopos pubescens*)				(1)	0.10	(3)	0.18
Orchard Oriole (*Icterus spurius*)				(1)	0.10	(1)	0.06
Tufted Titmouse (*Parus bicolor*)				(0.5)	0.05	(6)	0.36
Red-bellied Woodpecker (*Centurus carolinus*)						(8)	0.48
Great-crested Flycatcher (*Myiarchus crinitus*)						(7)	0.42
Wood Thrush (*Hylociehla mustelina*)						(5.5)	0.33
Red-eyed Vireo (*Vireo olivaceus*)						(4.5)	0.27
Northern Parula (*Parula americana*)						(4)	0.24
Red-headed Woodpecker (*Melanerpes erythrocephalus*)						(3)	0.18
Hairy Woodpecker (*Dendrocopos villosus*)						(3)	0.18
Eastern Wood Pewee (*Contopus virens*)						(3)	0.18

TABLE 1 (continued)

	Pasture	Cropland	Oldfield	Young forest	Mature hardwood forest
Scarlet Tanager (*Piranga olivacea*)					(3) 0.18
White-breasted Nuthatch (*Sitta carolinensis*)					(2) 0.12
Carolina Wren (*Thyrothorus ludovicianus*)					(2) 0.12
Acadian Flycatcher (*Empidonax virescens*)					(1) 0.06
Starling (*Sturnus vulgaris*)					(1) 0.06
Yellow-throated Vireo (*Vireo flavifrons*)					(1) 0.06
Yellow Warbler (*Dendroica petechia*)					(1) 0.06
Kentucky Warbler (*Oporornis formosus*)					(1) 0.06
Summer Tanager (*Piranga rubra*)					(1) 0.06
Total species	4	9	10	19	31
Males/ha	2.93	1.50	6.55	7.98	6.78
Species diversity (H′)	1.14	1.53	1.40	2.54	3.16
Equitability (J′)	0.83	0.70	0.61	0.86	0.92

(*Populus deltoides*), and walnut (*Juglans nigra*). Grass cover is present in open areas between the trees and is primarily muhly grass (*Muhlenbergia racemosa*), while the giant ragweed (*Ambrosia trifida*) is the most common forb. Woody species, mainly coralberry and elderberry (*Sambucus canadensis*) cover 22% of the oldfield. Grass is primarily *Bromus japonica* and sedges, and the most frequent forbs are giant ragweed, tall goldenrod (*Solidago altissima*) and the sunflower (*Helianthus* sp.). The pasture stand is almost entirely meadow fescue (*Festuca elatior*) and sweetclover (*Melilotus* sp.). About two-thirds of the cropland was planted in corn while the remaining portion had been planted in a cereal grain which had been overgrown by a mixture of oldfield grasses and forbs. A more detailed analysis of the vegetation is described by Tatschl and Bragg (1974).

RESULTS

Table 1 presents the data for the 5 habitats sampled during the breeding season, and Table 2 presents the winter populations on these same census plots. The Blue-gray Gnatcatcher (*Polioptila caerulea*), White-eyed Vireo (*Vireo griseus*), Black and White Warbler (*Mniotilta varia*), Prothonotary Warbler (*Protonotaria citrea*), Louisiana Waterthrush (*Seiurus motacilla*), and American Redstart (*Setophaga ruticilla*) were territorial at low densities in other parts of the mature hardwood forest stand.

DISCUSSION

As with grassland communities in general, the species diversity in the floodplain pasture is low in the breeding season and even lower in the winter (Tables 1 and 2). Because of poor drainage, the pasture is actually a wet meadow. Although the species composition in summer is similar to that in upland pastures of tall grass prairie, in the floodplain the Dickcissel and the Red-winged Blackbird are more abundant, while the Eastern Meadowlark and Grasshopper Sparrow have lower densities. Just the opposite is to be expected on upland sites.

During the breeding season in the cropland, only the Horned Lark is restricted to the plowed area planted in corn. Although portions of the corn were included within the territories of Dickcissels, Red-winged Blackbirds, Eastern Meadowlarks and the Indigo Bunting, most of their activities were centered in the third of the field overgrown by annual weeds. Thus the cropland bird population is similar to that of the oldfield; the species diversity index (H′) of the cropland (1.53) is close to that of the oldfield (1.40). In winter there is a greater difference in diversity. At this season the species diversity in the cropland is 0.85, while that of the oldfield is 1.98. This reflects the fact that since the vegetation of the cropland was primarily annuals and since the corn had been harvested, the habitat was more open and hence more climatically severe than the oldfield. Yet sufficient grain and weed seeds were available to support a surprisingly dense population of Eastern Meadowlarks.

Table 2

Winter Bird Populations of the Leavenworth Floodplain

	Pasture	Cropland	Oldfield	Young forest	Mature hard-wood forest
Size in hectares	8.0	14.0	20.2	10.4	16.7
Eastern Meadowlark (*Sturnella magna*)	(1)[1] 0.12[2]	(38)2.71			
Marsh Hawk (*Circus cyaneus*)	(1) 0.12	(1) 0.07	(3) 0.15		
Tree Sparrow (*Spizella arborea*)	(15)1.87	(6) 0.43	(24)1.19	(10)0.96	
Red-winged Blackbird (*Agelaius phoeniceus*)		(1) 0.07	(9) 0.45		
Common Flicker (*Colaptes auratus*)		(1) 0.07	(1) 0.05	(1) 0.10	(3) 0.18
Song Sparrow (*Melospiza melodia*)		(1) 0.07	(14)0.70	(4) 0.39	(1) 0.06
Downy Woodpecker (*Dendrocopos pubescens*)		(1) 0.07			(13)0.78
Swamp Sparrow (*Melospiza georgiana*)			(13)0.64		
Pine Siskin (*Spinus pinus*)			(7) 0.35		
Short-eared Owl (*Asio flammeus*)			(3) 0.15		
Loggerhead Shrike (*Lanius ludovicianus*)			(1) 0.05		
American Goldfinch (*Spinus tristis*)			(33)1.64	(3) 0.29	(1) 0.06
Black-capped Chickadee (*Parus atricapillus*)			(2) 0.10	(12)1.16	(11)0.66
Cardinal (*Cardinalis cardinalis*)			(1) 0.05		(5) 0.30
Bobwhite (*Colinus virginianus*)				(1) 0.10	
Tufted Titmouse (*Parus bicolor*)				(3) 0.29	(5) 0.30
Dark-eyed Junco (*Junco hyemalis*)				(2) 0.19	(8) 0.48

[1] individuals observed
[2] individuals/ha

TABLE 2 (continued)

	Pasture	Cropland	Oldfield	Young forest	Mature hard-wood forest
Red-bellied Woodpecker (*Centurus carolinus*)				(2) 0.19	(10)0.60
White-breasted Nuthatch (*Sitta carolinensis*)					(4) 0.24
Golden-crowned Kinglet (*Regulus satrapa*)					(3) 0.18
Red-headed Woodpecker (*Melanerpes erythrocephalus*)					(3) 0.18
Hairy Woodpecker (*Dendrocopos villosus*)					(2) 0.12
Blue Jay (*Cyanocitta cristata*)					(2) 0.12
Brown Creeper (*Certhia familiaris*)					(2) 0.12
White-throated Sparrow (*Zonotrichia albicollis*)					(1) 0.06
Total species	3	7	12	9	16
Individuals/ha	2.11	3.49	5.52	3.67	4.44
Species diversity (H′)	0.44	0.85	1.98	1.85	2.48
Equitability (J′)	0.40	0.44	0.80	0.84	0.89

As Margalef (1963) suggested and as Karr (1968) and Kricher (1972) have demonstrated, there is an increase in bird species diversity as communities are compared through the successional series to the climax community. Thus in the breeding season, the diversity index (H′) is 1.40 for the oldfield, 2.54 for the young forest, and 3.16 for the mature hardwood forest. This increase is less pronounced in winter when the structural complexity of the vegetation is reduced through leaf fall and by the decrease in herbaceous cover and when the weather is more severe (1.98, 1.85, and 2.48 respectively). That the diversity of the oldfield is actually greater in winter than in the summer appears to be a function of the abundance of a winter seed supply on the oldfield that supports a large population of wintering fringillids in mixed-species flocks as well as raptors like the Marsh Hawk and Short-eared Owl that feed upon seed-eating rodents. Furthermore, several forest species, for example the Black-capped Chickadee and Cardinal, moved into the oldfield to exploit this food supply.

The Shannon-Weaver diversity index is a function of 2 factors: species richness and the distribution of individuals among the species, the equitability. We used the measure of equitability (J') calculated by dividing the species diversity for the community by the maximum species diversity possible (the natural logarithm of the number of species in the sample) (Pielou 1966). Two patterns in equitability are apparent in Tables 1 and 2. One is the decrease in equitability from summer to winter in the pasture and cropland communities, the more structurally simple ones and the ones that are more affected by seasonal change. Although absolute values for equitability during the winter are lower in the young forest and mature hardwood forest, the differences are slight. This is perhaps correlated with the fact that the overall seasonal change in general structural complexity from summer to winter of woody vegetation is much less than with the herbaceous vegetation dominating the pasture and cropland sites. Kricher (1972) and Tramer (1969) suggest that the higher summer values reflect the spacing of individuals through territoriality, while the lower winter values are related to the greater variability and more stressful conditions of the winter climate. The higher equitability value for the oldfield in winter is due to the similar densities of Tree Sparrows, Song Sparrows, Swamp Sparrows, and American Goldfinches that make up the mixed-species flocks using the habitat and the relative stability of flock composition, as Kricher (1972) suggested was the case in his winter, oak forest community. The other pattern is the increase in equitability with successional stage from oldfield to young forest to mature hardwood forest in both summer and winter. A similar trend was noted by Kricher (1972), and again, the lower equitability values may be related to the greater instability of the earlier seral stages. The observation by Emlen (1972) that low equitability was associated with disturbance of the habitat supports this suggestion.

Census data from climax floodplain forests in Illinois (Karr 1968) and Maryland (Criswell, et al. 1973 and previous years) provide for geographic comparisons with the Leavenworth site. The Rose-breasted Grosbeak, which was the second most abundant species at Leavenworth, did not occur in either the Illinois or Maryland censuses. Although the Kansas densities were low, the Orchard Oriole, Yellow Warbler, and Summer Tanager similarly were not present in the floodplain forest censuses further east. Other species show a higher density in Kansas than in the east. For example, the density of the Great Crested Flycatcher in Maryland for the last 10 years the census has been published is 0.33 males/ha and in Illinois it is 0.32 males/ha, while at Leavenworth the density is 0.42 males/ha. The Northern Oriole is missing from the Maryland avifauna, has a density of 0.15 males/ha in Illinois, but a density of 0.48 males/ha at Leavenworth. The major generalization that

can be seen in these data, however, is the decrease in species densities towards the west. The combined densities of the parids (*P. carolinensis* and *P. bicolor*) in Maryland is 1.2 males/ha (10-year average) and in Illinois it is 1.4 males/ha. At Leavenworth it is only 0.72 males/ha (*P. atricapillus* and *P. bicolor*). As should be expected, the decreasing trend is even more evident in typical eastern deciduous forest species. In Maryland the Red-eyed Vireo has a density of 1.7 males/ha (10-year average), in Illinois, 0.32 males/ha, and at Leavenworth only 0.27 males/ha. The Acadian Flycatcher drops from 1.4 males/ha in Maryland (10-year average) to 0.57 males/ha in Illinois to 0.06 males/ha at Leavenworth. The Northern Parula, Eastern Wood Pewee, Downy Woodpecker, and Starling generally show a similar pattern.

The number of species present in the mature floodplain forest is a little lower in Maryland (25 species, 10-year average) and similar in Illinois and Leavenworth (32 and 31 species respectively), but the decrease in density is quite definite from east to west. The 10-year average in the Maryland forest is 15.04 males/ha, while in Illinois the total density is 12.08 males/ha. At Leavenworth the density is only 6.76 males/ha.

SUMMARY

Bird populations were censused in both summer and winter in pasture, cropland, old-field, young forest, and mature hardwood forest habitats at Fort Leavenworth, Kansas on the floodplain of the Missouri River.

In both summer and winter, species diversity was lowest in the pasture, low in the cropland, and increased through the successional habitats to the mature hardwood forest. Equitability was higher in summer than in winter in the cropland and pasture habitats and increased with the successional stage.

A comparison with breeding-bird census data from mature floodplain forests in Maryland and Illinois revealed that species richness did not vary greatly with longitude, but that the density of territorial males decreased markedly from east to west. Although some species reached their highest densities in the Leavenworth forest, this trend in overall density reflects the general westward decrease of species characteristic of the eastern deciduous forest.

ACKNOWLEDGMENTS

This study was supported by contract No. DACW4173CO112 from the U.S. Army Corps of Engineers. Permission to conduct the research on Fort Leavenworth was granted through the courtesy of the Commander, Headquarters, Fort Leavenworth.

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DIVISION OF BIOLOGY, KANSAS STATE UNIV., MANHATTAN 66506. ACCEPTED 22 OCT. 1974.

NEW LIFE MEMBER

Professor Robert A. Whiting has recently become a life member of the Wilson Ornithological Society. Professor Whiting teaches Ornithology and Conservation of Natural Resources at Jackson Community College, Jackson, Michigan. He is the author of publications on wildlife photography and Michigan birds, including "Enjoying Birds in Michigan," which is now in its second edition. Professor Whiting has been very active in the Michigan Audubon Society for over 30 years. He has served as that society's president, as a member of its board, and he originated the Michigan Audubon Society endowment fund. Professor Whiting and his wife, Marie, enjoy bird-watching, canoeing, bird-photography, and traveling.

DEVELOPMENT OF YOUNG BREWER'S BLACKBIRDS

Martha Hatch Balph

Brewer's Blackbirds (*Euphagus cyanocephalus*) are common in much of the western U.S. Several workers have studied aspects of the breeding behavior of this species (LaRivers 1944; Howell and Bartholomew 1952; Williams 1952; Horn 1968, 1970). However, there appears to be little published information on the development of young Brewer's Blackbirds. The objective of this paper is to present some findings on this topic, and where possible to compare Brewer's Blackbird development with that of other passerines, particularly members of the family Icteridae.

METHODS

I observed free-living, young Brewer's Blackbirds in Logan, Utah, during late May and June, 1973 and collected data from 41 nestlings aged 0–13 days at 10 nests. Of these birds, 37 were of known age, and four were of estimated age. The nests were in urban situations, varying from hedgerows bordering lawns to brushy roadside vegetation.

I removed the birds from their nests for about 10–20 min to examine them. I weighed them to the nearest 0.1 g on a triple-beam balance and measured linear growth parameters with calipers to the nearest 0.5 mm; these parameters included the wing, first primary, central rectrix, culmen, commissure, tarsus, and hallux. Notations of plumage development and of the condition and coloration of soft parts were made without the use of a color chart. I also documented behavior at my approach to young in the nest or young away from their nests. I recorded the birds' ages as "day 0" during the first 24 hours after hatching, as "day 1" from 24–48 hours, and so forth. Nestlings were individually marked on the tarsi or feet with a felt-tipped marker or with fingernail polish until they were about 1 week old, when they were banded.

Data were collected between 07:00 and 18:30, 35% in the morning and 65% in the afternoon. I visited individual nests at approximately the same time each day, but was unable to collect data at all active nests on all days. Nest losses, due apparently to predation and flooding, and fledging of young after the age of 9 days caused progressive reductions in sample size. On five occasions, I captured and collected data from banded young 1–2 days after they fledged.

For purposes of comparison, I measured 10 adult Brewer's Blackbirds (five males, five females) captured in Logan in June, 1974.

I obtained supplementary data on behavioral ontogeny from an earlier study of captive young. On 18 June 1967, I collected four Brewer's Blackbird nestlings at the approximate age of 5 days in Laramie, Wyoming. These were hand fed a mixture of hydrated Gerber's high protein pablum, strained beef, ground egg with eggshell, honeybee larvae, small flying insects, and earthworms. When the birds began to feed themselves, I added canned dog food, millet seed, mealworms, and grit to their diet. Water was provided beginning at 15 days.

I kept the birds in their original nest until they fledged. After they fledged, I maintained them in a $56 \times 51 \times 38$ cm cage and released them daily for 1–3 hours into a

Table 1

Measurements of Adult Brewer's Blackbirds

Measurement	Males (n = 5)		Females (n = 5)		Both Sexes (n = 10)	
	$\bar{X}$	SD	$\bar{X}$	SD	$\bar{X}$	SD
Weight (g)	69.7	2.91	60.4	6.06	65.1	6.64
Wing Chord (mm)	135.0	4.47	122.2	2.17	128.6	7.52
First Primary (mm)	82.4	3.19	76.5	1.58	79.4	3.91
Central Rectrix (mm)	102.8	3.56	91.4	2.61	97.1	6.69
Exposed Culmen (mm)	21.1	0.55	19.4	1.08	20.2	1.21
Culmen, Nostril to Tip (mm)	14.5	0.87	13.1	0.65	13.8	1.03
Commissure (mm)	12.5	0.61	12.0	0.79	12.2	0.72
Tarsus (mm)	33.3	1.10	32.2	0.98	32.8	1.14
Hallux (mm)	20.7	0.45	20.6	1.02	20.6	0.75

6.1 × 3.7 × 2.4 m room. I monitored behavioral development of four birds (two males, two females) from 5–12 days and three birds (one male, two females) from 13–42 days.

MORPHOLOGICAL DEVELOPMENT

Information on morphological development is from free-living Brewer's Blackbirds. The results are presented and discussed in this section under the broad headings of growth, plumage development, and condition and coloration of soft parts.

Growth.—Ten recently hatched nestlings, weighed while the down was still wet and probably before their first feeding, averaged 3.7 g (SD = 0.32). Of birds in this sample, three were known to be less than 5 min old and likewise averaged 3.7 g (SD = 0.12). The mean weight of newly hatched Brewer's Blackbirds was 6% that of adult females (Table 1), which is in general agreement with findings for other icterids (Holcomb and Twiest 1968).

Nestlings weighed on day 0 after the down was dry averaged 4.4 g (Fig. 1). The birds gained weight rapidly during the first few days of nestling life. Daily weight gains peaked at 5.8 g on day 5, then decreased to less than 3 g during the second half of the nestling period. Percentage daily increases were greatest ($\geq 48\%$) up to day 3, then dropped off sharply and were less than 10% from day 8 on. At 10 days, the birds averaged 70% of adult female weight, which agrees with observations for other passerines (Nice 1943).

Individual variability in weight was attributable partly to asynchronous hatching. At seven nests where the hatching times of the first and last eggs were known to be separated by 24–48 hours, first- and last-hatched birds weighed nearly the same on day 0. After day 0, those first hatched

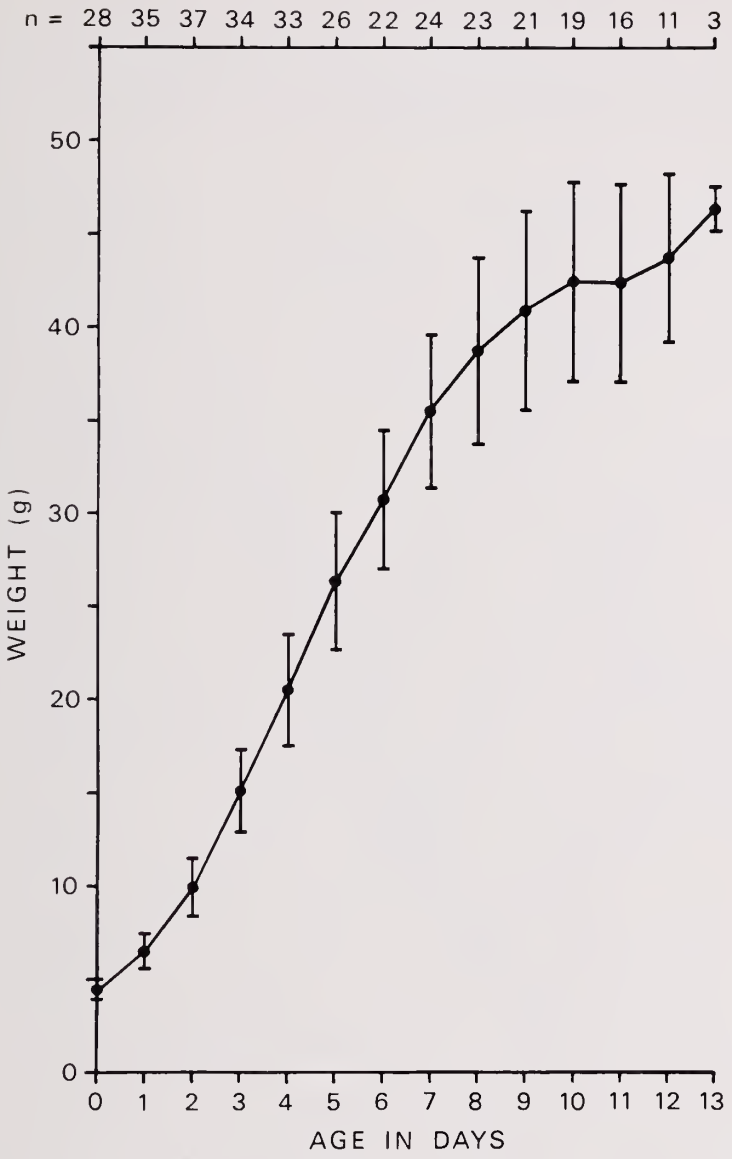


FIG. 1. Relationship between body weight and age in young Brewer's Blackbirds. Dots represent means; brackets indicate mean ± one standard deviation.

weighed more than those last hatched (Fig. 2). The difference was not great, but it was consistent. Presumably, later hatched birds were at a competitive disadvantage during feeding. If food were in short supply, these younger birds might be expected to die. Such brood reduction may be beneficial to

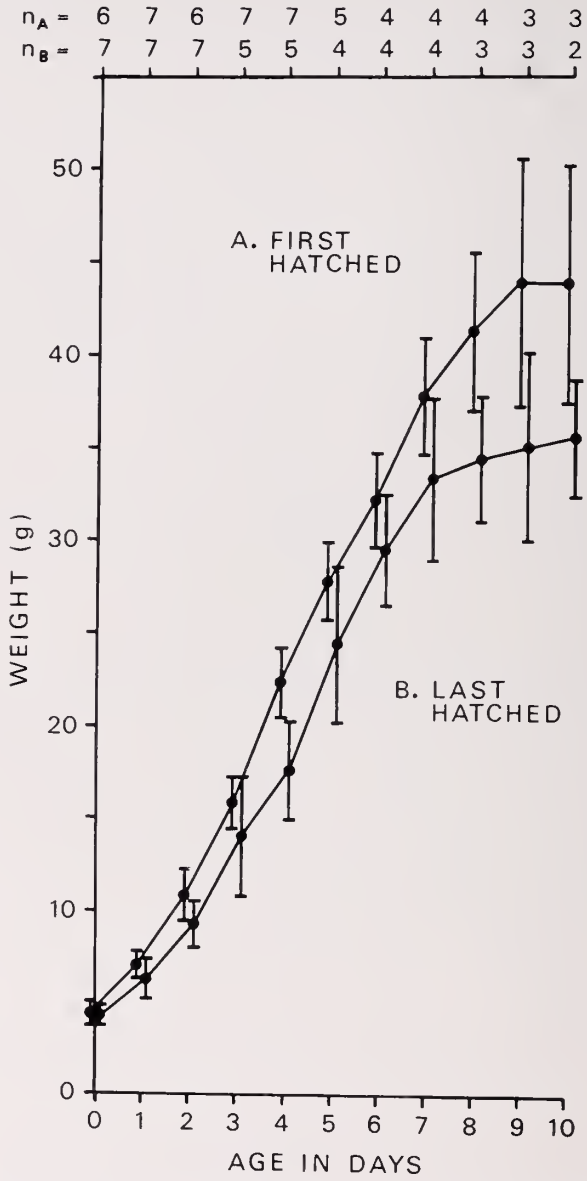


FIG. 2. Relationship between body weight and age in (A) first-hatched and (B) last-hatched Brewer's Blackbirds of asynchronously hatched broods. Dots represent means; brackets indicate mean ± one standard deviation.

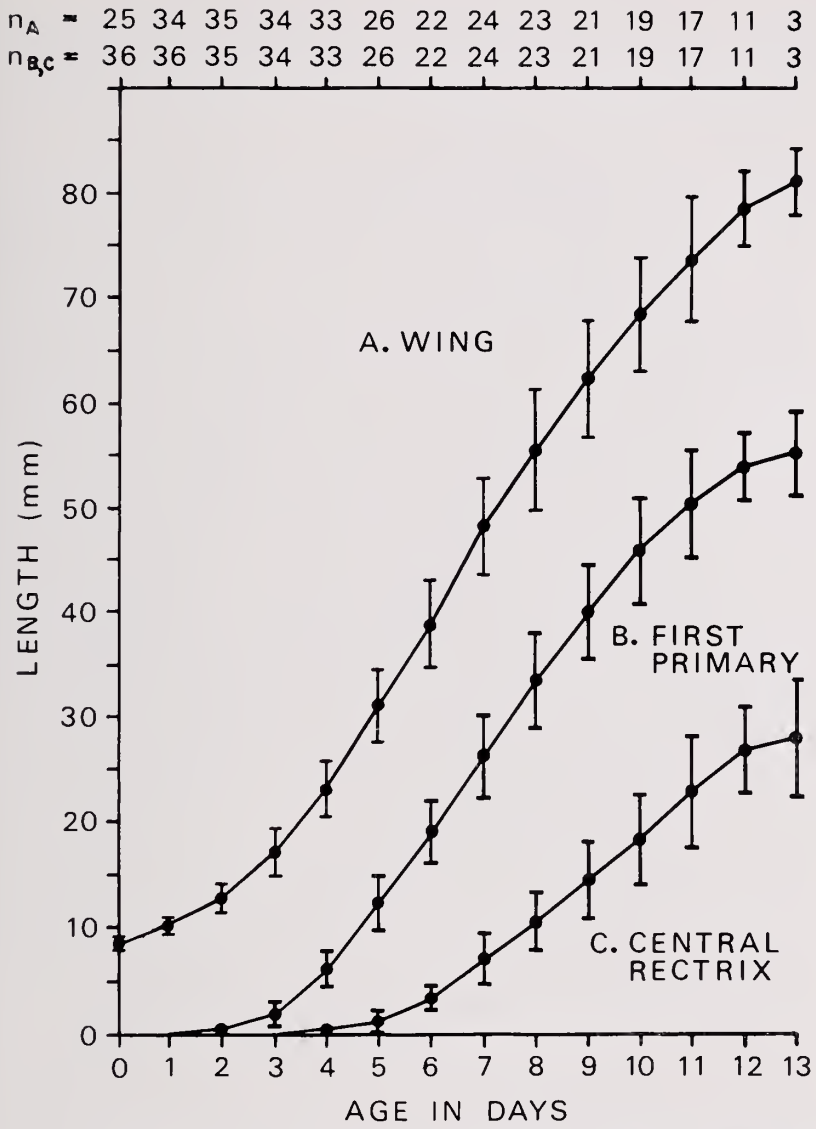


FIG. 3. Relationship between age and (A) wing chord, (B) length of first primary, and (C) length of central rectrix in young Brewer's Blackbirds. Dots represent means; brackets indicate mean ± one standard deviation.

species occupying habitats with unpredictable fluctuations in food availability (Lack 1954, Ricklefs 1965). Some factors besides asynchronous hatching which might have contributed to variation in weight between birds were: (1) sexual dimorphism; (2) differences in brood size, which ranged

from 3–6: (3) differences in the spatial distribution of nests affecting the foraging success of adults (Horn 1968): (4) fluctuating weather conditions affecting food availability: (5) differences in the time of day at which birds from different broods were weighed.

The wing, held half open and measured along the chord, followed a sigmoidal growth pattern (Fig. 3). Its daily growth increased during the first half of the nestling period, peaking at 9.2 mm on day 7, then decreased gradually through the second week of nestling life. By day 13, the wing chord was 63% that of adults.

The right innermost primary and rectrix were measured from the point of emergence through the skin to the distal tip. The first primary emerged through the skin on days 2–3 (Fig. 3). Its daily growth was greatest on days 5–9, peaking at 7.4 mm on day 7. The central rectrix emerged 2 days later than the first primary and showed smaller daily increases until very late in nestling life. Then, its daily increment slightly exceeded that of the first primary. By day 13, the first primary had attained 69% of its full growth, whereas the central rectrix was only 28% of adult size.

Three parameters of bill growth were measured: (1) culmen, from the skin of the forehead to the tip of the upper mandible: (2) culmen, from the anterior corner of the nostril to the tip of the upper mandible: (3) commissure, from one commissural point to the other with the bill closed. The exposed culmen increased an average of 0.8 mm daily during the first week of nestling life, lessening to 0.5 mm daily during the second week (Fig. 4). Growth of the culmen from nostril to tip was uniform (about 0.4 mm daily) throughout the nestling period. Daily growth of the commissure exceeded that of the culmen (both measurements) on days 1–4, then dropped below that of the culmen on days 5–7. During the second week, the commissure decreased slightly as the oral flanges became less prominent. These findings are in keeping with those of Holcomb and Twiest (1968) for Red-winged Blackbirds (*Agelaius phoenicius*). Holcomb and Twiest (1968) have pointed out that the development of a large gape early in nestling life provides a good feeding stimulus for the parent, while progress toward a more pointed bill shape later in the nestling period prepares birds for adult foraging.

The tarsus was measured from the point of the joint between the tibia and tarsometatarsus, to the base of the middle toe anteriorly. The hallux was measured dorsally from the point of its articulation with the accessory metatarsal to the tip of the extended claw. Growth of the tarsus and of the hallux (Fig. 5) followed a sigmoidal pattern with the greatest increases on days 3 and 4. Percentage daily increases were greatest (20–29%) during the first 4 days of nestling life and decreased thereafter. The tarsus and the hallux attained 50% of their full growth by days 3–4 and were close to adult size

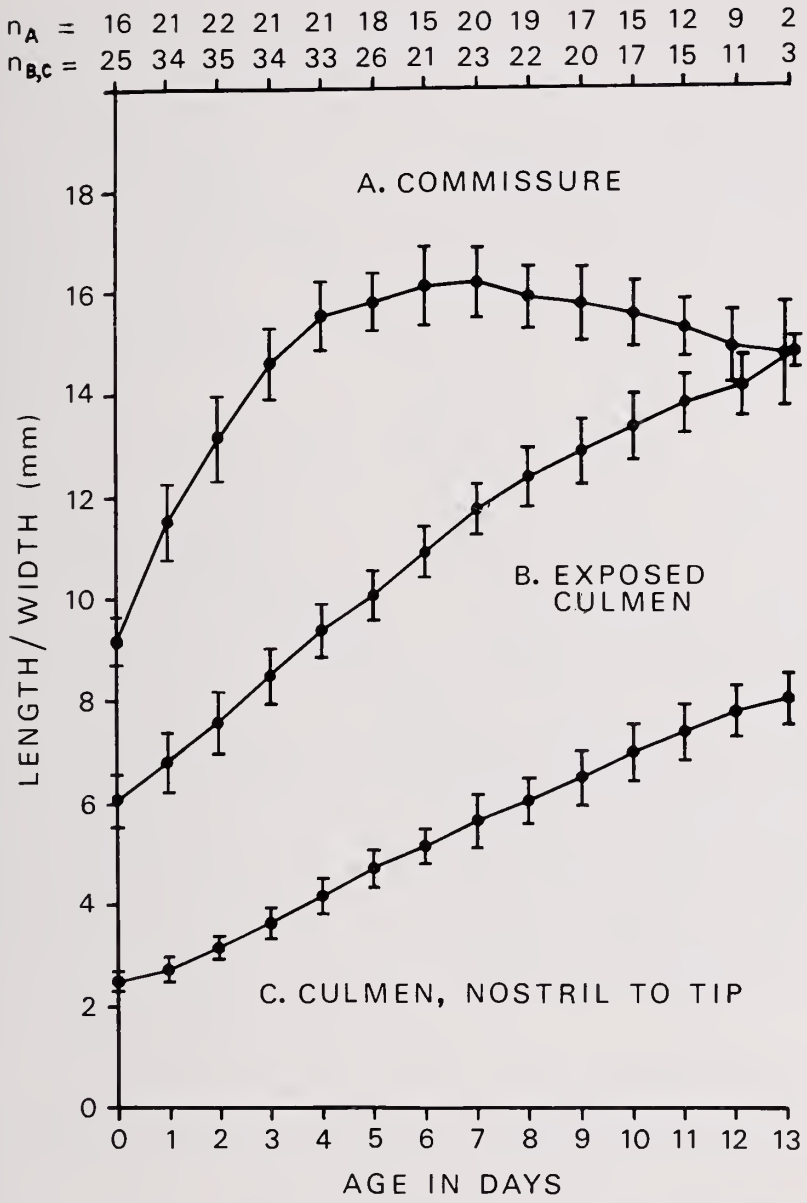


FIG. 4. Relationship between age and (A) width of commissure, (B) length of exposed culmen, and (C) length of culmen, nostril to tip in young Brewer's Blackbirds. Dots represent means; brackets indicate mean ± one standard deviation.

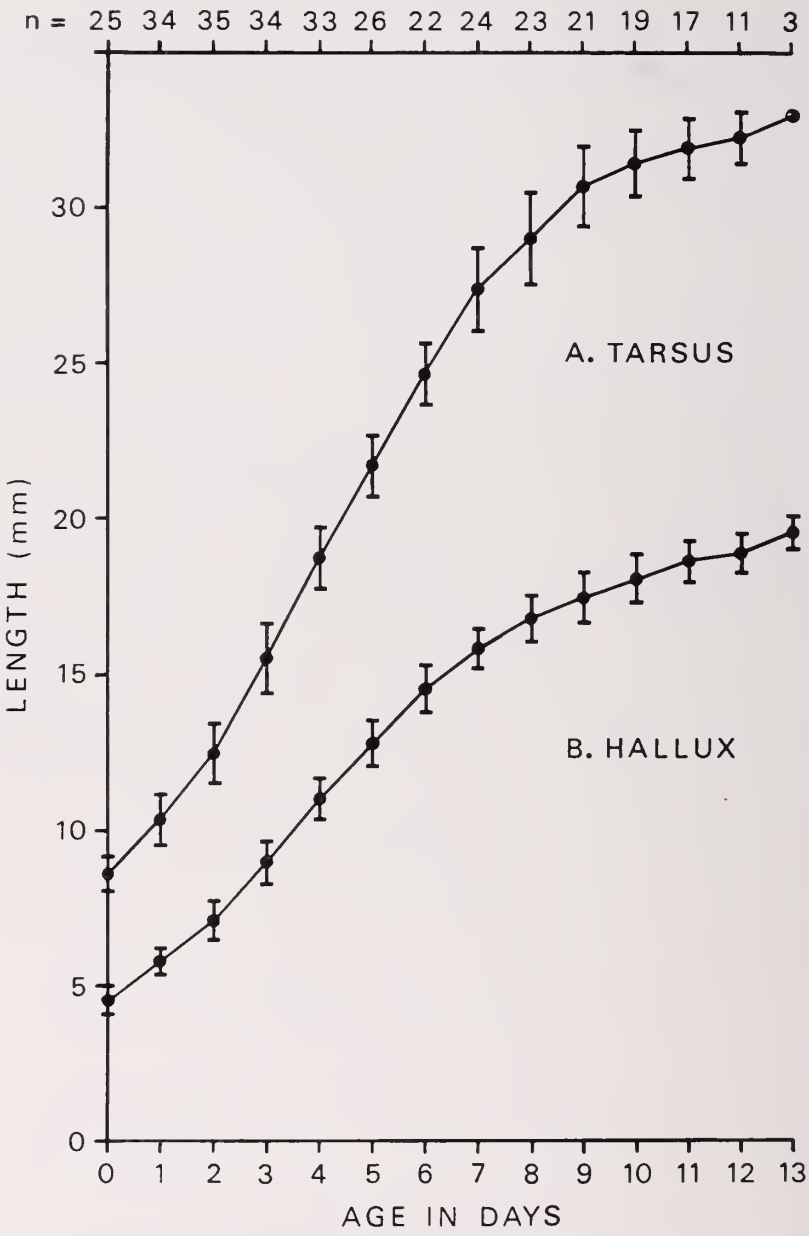


FIG. 5. Relationship between age and length of (A) tarsus and (B) hallux in young Brewer's Blackbirds. Dots represent means; brackets indicate mean ± one standard deviation.

TABLE 2

MAXIMUM LENGTH AND PERCENTAGE OCCURRENCE OF NEOSSOPTILES IN VARIOUS TRACTS OF 23 BREWER'S BLACKBIRDS AGED 0 DAYS

Tract	Region	Maximum Length (mm) $\bar{X}$	Maximum Length (mm) SD	Percentage Occurrence
Capital	Coronal	9.0	1.05	100
Capital	Occipital	8.7	1.15	100
Spinal	Dorsal	10.9	1.35	100
Spinal	Pelvic	7.8	1.41	100
Ventral	Abdominal	1.8	1.33	74
Humeral	—	11.7	1.33	100
Femoral	—	8.8	0.90	100
Crural	—	3.0	0.94	100
Alar	Primaries or Upper Greater Primary Coverts	0.6	0.39	87
Alar	Upper Greater Secondary Coverts	9.7	0.21	100
Alar	Upper Middle Secondary Coverts	9.7	0.21	100
Alar	Alula	0.3	0.41	44
Caudal	Rectrices	2.9	1.36	100

by day 10. Holcomb and Twiest (1968) observed similar, rapid growth of the legs and feet in Red-winged Blackbirds. Development of the legs and feet contributes to a nestling's ability to stretch for food and to grasp and balance (Holcomb and Twiest 1968). In addition, birds reared within the reach of ground predators are under selective pressure to be able to walk from the nest before they can fly (Beason and Franks 1973). Brewer's Blackbirds place their nests in a variety of situations, including on or near the ground where they are subject to heavy predation pressure (LaRivers 1944). Rapid tarsal relative to wing development in this species may have evolved partly in response to this pressure.

Plumage development.—Nestlings were sparsely covered with pale, grayish-white down on day 0. This observation differs from Linsdale (1936), who describes down color in Brewer's Blackbird nestlings in Nevada as "nearly black." Neossoptiles were most abundant in the capital, spinal, humeral, and femoral tracts, and in regions of the future upper greater and middle secondary coverts in the alar tract. Down lengths on day 0, calculated for the longest neossoptile of each tract or region, were greatest in the humeral tract and in the dorsal region of the spinal tract (Table 2). These findings agree generally with those of Wetherbee (1957) for several other icterids.

Neossoptiles were least abundant in, and were sometimes absent from, the abdominal region of the ventral tract and regions of the future primaries, greater primary coverts, and alulae. The presence or absence of natal down in the abdominal region on day 0 tended to be consistent within broods. In four of five broods examined, 75–100% of siblings had neossoptiles in the abdominal region; whereas in the fifth brood, all nestlings lacked down in this region. Saunders (quoted in Wetherbee 1957) observed a similar phenomenon in newly hatched Brewer's Blackbirds. Although I cannot be certain that the lack of abdominal down in some nestlings in the present study was not due to abrasion, the high degree of similarity among siblings suggests that genetic mechanisms may have been responsible for the variation observed.

Down was lost during the nestling period from the extremities and usually from the crural tract and abdominal region, but vestiges remained attached elsewhere through fledging. On day 12, all but one of 10 birds had neossoptiles still attached to the tips of juvenal feathers in the capital, spinal, humeral, and femoral tracts, and to the tips of upper greater and middle secondary coverts.

Development of the juvenal plumage was categorized as follows: (1) dark papillae not yet visible under skin; (2) dark papillae visible but not yet erupted through skin; (3) sheaths emerging through skin (to 1 mm out of skin); (4) sheaths more than 1 mm out of skin but not yet broken; (5) feathers breaking through sheaths; (6) feathers out of sheaths but of lesser length than sheaths; (7) feathers out of sheaths and of greater length than sheaths. If feathers in a particular region were at more than one stage of development, the median stage was recorded. Ten birds were examined in each age group; these represented a total of 28 individuals.

On day 0, papillae of the primaries were marked by dark pigment in all birds (Table 3). Five of 10 birds also showed darkening of papillae of the alulae and secondaries. Papillae in the spinal and ventral tracts were faintly discernible as unpigmented dots. On days 1 and 2, dark papillae became evident in the spinal, ventral, humeral, femoral, and crural tracts; in the caudal tract (rectrices); and in upper regions of the alar tract. Primaries, and in some birds alulae and secondaries, emerged through the skin on day 2. Emergence of secondaries, and usually of primaries (seven of 10 birds), began distally and proceeded proximally.

Days 3–5 marked the emergence of sheaths through the skin in many regions. By day 5, sheaths were prominent in the spinal, ventral, humeral, femoral, and crural tracts; in the alar tract (primaries, alulae, secondaries, and upper coverts); and in the caudal tract (rectrices, developing from outermost to innermost). Dark papillae were evident in remaining regions of the alar and caudal tracts and in the capital tract.

Table 3

Development of the Juvenal Plumage[1] in Brewer's Blackbirds from 0–12 Days (N = 10)

Tract/Region	Age in Days												
	0	1	2	3	4	5	6	7	8	9	10	11	12
Capital													
Frontal	A	Ab	ab	B	B	B	C	Cd	De	dE	E	eF	Fg
Coronal	A	Ab	ab	B	B	Bc	cd	D	De	Ef	Fg	fG	G
Occipital	A	A	aB	B	B	Bc	cd	De	E	F	fG	G	G
Superciliary	A	A	A	Ab	aB	B	Cd	cD	D	De	def	F	Fg
Auricular	A	A	A	A	aB	bC	cd	D	De	dE	E	eF	Fg
Postauricular	A	A	A	Ab	B	B	bC	cD	dE	Ef	F	Fg	G
Interramal	A	A	A	A	ab	B	B	C	cD	De	E	ef	Fg
Malar	A	A	A	A	aB	B	B	Cd	D	De	def	efg	fG
Submalar	A	A	A	Ab	B	B	Bc	cD	D	dEf	eF	fG	G
Spinal													
Cervical	A	B	B	B	bC	Cd	D	dE	ef	F	fg	G	G
Interscapular	A	B	B	Bc	C	D	De	E	F	F	fg	G	G
Dorsal	A	Ab	B	B	bC	D	De	Ef	F	F	fG	G	G
Pelvic	A	Ab	B	B	Bc	cD	D	E	F	F	Fg	fG	G
Ventral													
Cervical	A	Ab	B	B	C	D	De	E	eF	Fg	fG	G	G
Sternal	A	Ab	B	B	Cd	D	dE	eF	F	Fg	fG	G	G
Axillar	A	A	A	B	B	bC	cd	de	E	F	Fg	fG	G
Abdominal	A	A	B	B	C	D	dE	Ef	F	F	Fg	fG	G
Humeral	A	B	B	Bc	Cd	D	dE	Ef	F	Fg	G	G	G
Femoral	A	aB	B	B	Cd	D	dE	Ef	F	Fg	G	G	G
Crural	A	Ab	B	B	bC	cD	dE	E	ef	Fg	fG	G	G
Alar													
Primaries	B	B	C	cD	D	D	E	F	F	F	F	fG	G
Secondaries	ab	B	Bc	cD	D	D	E	F	F	F	F	fG	G
Alula	ab	B	bC	cD	D	De	def	F	F	Fg	fg	G	G
Upper Greater Primary Coverts	A	Ab	Bc	Cd	D	D	De	E	eF	Fg	fG	G	G

TABLE 3—*Continued*

Tract/Region	Age in Days												
	D	1	2	3	4	5	6	7	8	9	10	11	12
Upper Middle Primary Coverts	A	A	aB	B	bC	cD	De	E	eF	fg	G	G	G
Upper Greater Secondary Coverts	A	ab	B	cd	D	D	De	Ef	F	Fg	G	G	G
Upper Middle Secondary Coverts	A	Ab	B	Bc	Cd	D	De	Ef	F	fg	G	G	G
Under Greater Primary Coverts	A	A	A	A	A	A	A	abc	aD	def	adef	dfg	ef
Under Middle Primary Coverts	A	A	A	A	A	A	Bc	bcd	bde	cE	dfg	fg	fG
Under Greater Secondary Coverts	A	A	A	A	Ab	Ab	D	dE	def	F	fG	G	G
Under Middle Secondary Coverts	A	A	A	Ab	aB	bc	cd	cD	dE	E	efg	fg	fG
Under Lesser Secondary Coverts	A	A	A	Ab	aB	aB	bC	cD	De	Eg	fg	G	G
Marginal Coverts	A	Ab	B	Bc	C	cD	De	E	Ef	efg	fG	fG	G
Carpometacarpal Coverts	A	A	Ab	aB	B	bc	Cd	cD	dE	eF	Fg	G	G
Caudal													
Rectrices	A	Ab	B	B	bC	cD	de	E	ef	F	F	F	F
Upper Tail Coverts	A	A	Ab	B	Bc	Cd	De	E	eF	F	F	Fg	G
Under Tail Coverts	A	A	A	aB	B	bc	D	D	Ef	F	F	Fg	G
Postventral	A	A	A	aB	B	bc	cD	de	Ef	F	Fg	fG	G
Anal Circlet	A	A	A	Ab	B	B	bcd	dE	E	eF	fG	G	G

[1] The stages of development of the juvenal plumage are coded as follows: A,a = no dark papillae; B,b = dark papillae visible beneath skin; C,c = sheaths emerging through skin; D,d = sheaths > 1 mm out of skin; E,e = feathers rupturing sheaths; F,f = feathers out of sheaths but of lesser length than sheaths; G,g = feathers out of sheaths and of greater length than sheaths. Capital letters indicate 60-100 percent of birds; small letters indicate 20-50 percent of birds.

TABLE 4

PERCENTAGE OF YOUNG BREWER'S BLACKBIRDS OPENING THEIR EYES TO VARYING DEGREES WITH INCREASING AGE

Age in Days	n	Maximum Parting of Eyelids (mm)					
		0.0	0.5	1.0	2.0	3.0	4.0
0	29	100	0	0	0	0	0
1	34	88	12	0	0	0	0
2	35	51	40	9	0	0	0
3	34	9	50	29	12	0	0
4	33	0	0	67	33	0	0
5	26	0	0	8	81	11	0
6	22	0	0	0	50	50	0
7	24	0	0	0	21	71	8
8	23	0	0	0	0	48	52
9	21	0	0	0	0	5	95
10	19	0	0	0	0	0	100

On day 6, primaries broke through the distal portions of their sheaths. Similar timing of primary rupture has been described in several other passerines, including Red-winged Blackbirds (Holcomb and Twiest 1970), House Sparrows (*Passer domesticus*) (Weaver 1942), and Rufous-sided Towhees (*Pipilo erythrophthalmus*) (Barbour 1950). Rupture of other teleoptiles occurred in the more advanced tracts and regions on days 6–7, and in remaining regions by day 10. Apteria associated with the spinal tract were concealed by teleoptiles by days 7–8. Overlapping of the mid-ventral apterium proceeded more slowly, particularly on the lower abdomen, but was complete by day 12 in most birds. Daily weight gains decreased during this period of rapid feather production, as in many other passerine species (Banks 1959, Holcomb 1968, Holcomb and Twiest 1968, Bateman and Balda 1973).

Condition and coloration of soft parts.—The eyes of all birds were closed on day 0 (Table 4). On days 1–3, nestlings began to open their eyes slightly while gaping. By days 8–9, the birds were alert and kept their eyes open for extended periods in my presence.

The irides of all nestlings were dark brown when the eyes first opened. By days 12–13, four of 11 birds had minutely paler irides than others of the same age and probably were males. A hand-raised male had grayish-white irides by the age of 3 weeks.

The mouth lining was bright pink or red, which is typical in nestling icterids (Ficken 1965). The mouth lining became tinged with grayish near the end of the nestling period, thus changing toward the black color in adults.

The tongue was pale in young nestlings but darkened posteriorly after day 9. The skin was a bright, yellowish pink on day 0, and the abdominal viscera were clearly visible through it. The skin became thicker, more wrinkled, and dull in hue through the course of the nestling period.

The nestlings' bills, tarsi, feet, and claws were pale at hatching and darkened to the black color of adult structures by fledging. The bill was predominantly flesh-colored, grayish near the tip, on days 0–1. The prominent oral flanges and the egg tooth were white. The bill became darker and grayer than body skin, markedly so toward the tip, on days 2–3. The bill continued to darken through the nestling period, until by day 12 it was nearly black. During the latter part of nestling life, the flanges regressed somewhat and became grayish. The egg tooth was inconspicuous after about the first week, but a remnant was still discernible at 13 days.

The tarsi and feet were flesh-colored, and the claws white, on days 0–1. The tarsi and feet became perceptibly darker and grayer than body skin on days 3–4 and were nearly black by days 10–11. Slight proximal darkening of the claws was evident by days 2–3. By day 5, the claws were medium gray proximally and pale gray or white distally; and by days 10–11 they were black.

BEHAVIORAL DEVELOPMENT

The development of activities in free-living Brewer's Blackbirds from 0–13 days, and in captives from 5–12 days, is summarized in Table 5. Behavior is described and discussed in this section within several general categories: responses concerned with nutrition, body maintenance, locomotion and related activities, escape responses, social behavior, and vocalizations.

Responses concerned with nutrition.—Three nestlings observed at hatching first gaped when they were 2–4 min old. During the early part of the nestling period, birds gaped when I gently shook them, touched their nests, or made lip-smacking sounds. Young nestlings always gaped vertically; however, at 7–9 days the birds began to orient their gaping toward siblings or toward a pointed object moved from side to side several cm from their heads. A few days later, they began to flutter their wings while begging. Free-living birds gaped less readily in my presence toward the end of nestling life than they did earlier, probably because of increasing ability to discriminate between reinforcing and non-reinforcing stimuli.

Independent feeding responses developed near the time of fledging. I first saw bill-wiping by a wild bird on day 10 and by hand-raised birds on day 12. Exploratory pecking appeared in hand-raised birds on day 14. The birds initially directed pecks toward various objects which contrasted visually with the background, but by the age of 4–5 weeks they pecked exclusively at edible objects. At 3–4 weeks, the birds were able to catch insect prey and

Table 5

Onset and Duration of Activities in Young Brewer's Blackbirds, Free-living (———) Observed from Days 0–13 and Hand-raised (----------) Observed from Days 5–42

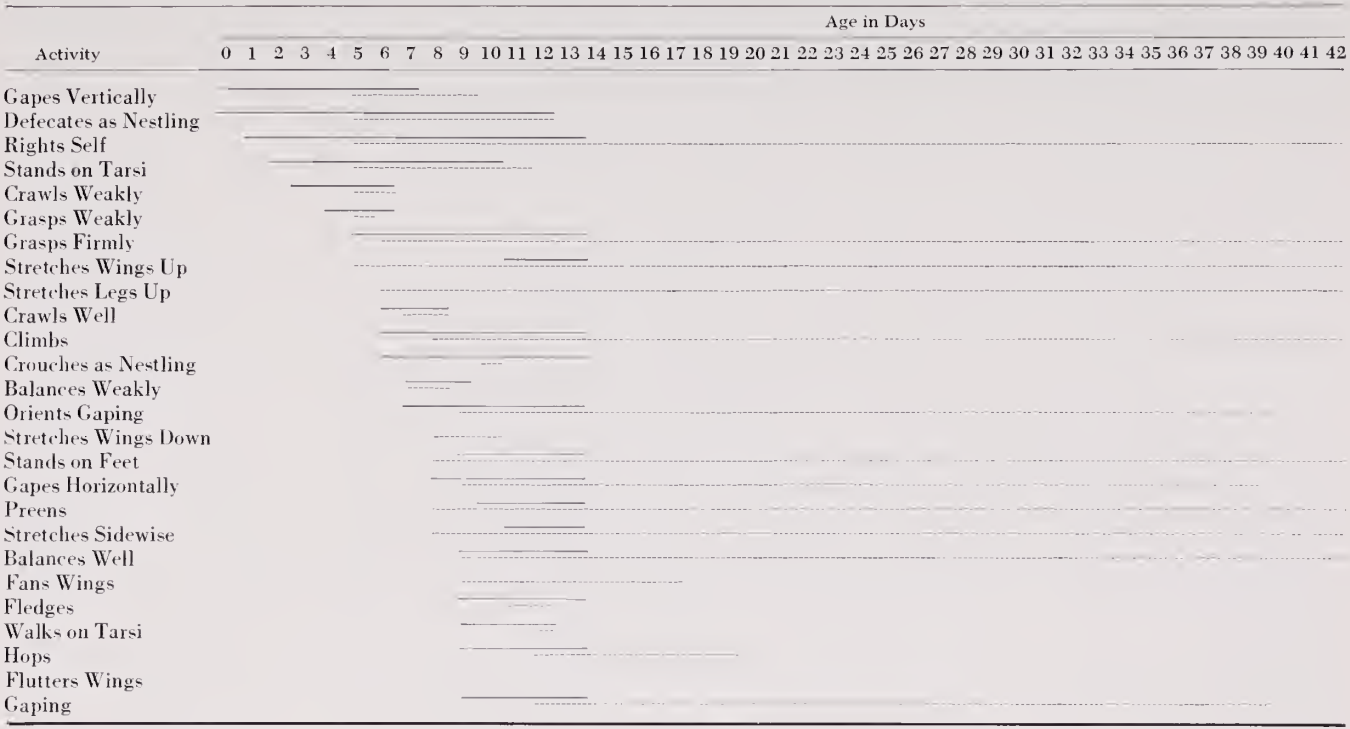
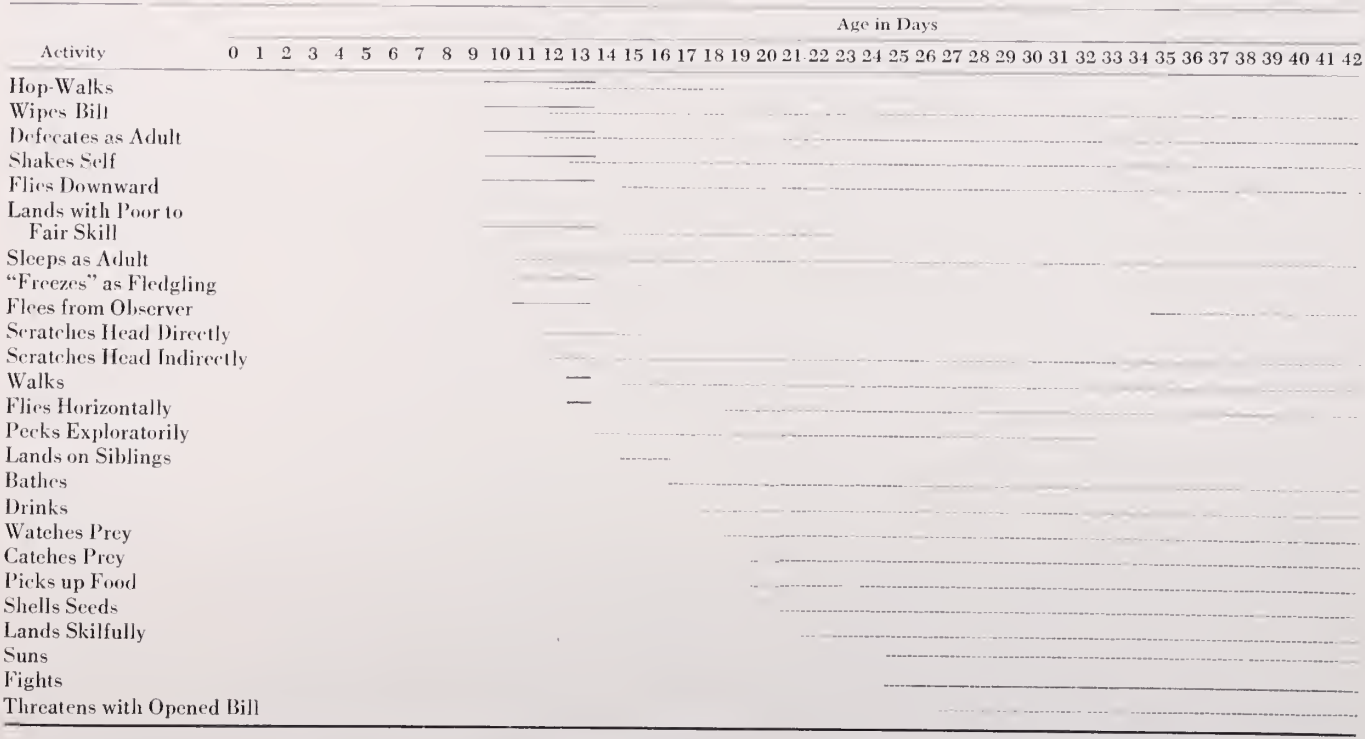


TABLE 5—*Continued*



to pick up and shell millet seeds: however, they showed these behaviors when they were only slightly hungry. As time since the last hand feeding increased, they reverted to begging. Similar findings have been reported for other altrices beginning to feed independently (Nice 1943). By day 39, hand-raised birds attained complete independence in feeding, which agrees with Williams' (1952) observations of free-living Brewer's Blackbirds.

Defecation by hand-raised nestlings was directed upward but was not typically over the side of the nest. Droppings were in the form of fecal sacs until fledging when the membranous covering was lost. Feeding and handling stimulated defecation in nestlings but not in fledglings.

Free-living and hand-raised birds occasionally regurgitated undigested food in the form of pellets 1–2 cm in length. I observed this phenomenon three times in wild birds aged 11–12 days and nine times in captives aged 6–28 days. Two pellets regurgitated by free-living nestlings contained small pebbles ($\leqslant 3 \times 2$ mm), bits of eggshell and snailshell ($\leqslant 4 \times 2$ mm), undigested hard insect parts ($\leqslant 5 \times 3$ mm), a 3 mm thorn, and strands of fibrous plant material ($\leqslant 26$ mm in length). Regurgitation of pellets has been observed in nestling Common Crows (*Corvus brachyrhynchos*) (Parmalee 1952) and in a 33-day-old Bobolink (*Dolichonyx oryzivorus*) (pers. obs.), as well as in adult corvids (Harlow 1922, and others).

Body maintenance.—My observations of body maintenance activities were primarily on captive birds. However, I did record preening, stretching, and shaking by a few free-living nestlings, beginning on days 10–11.

Hand-raised birds began to preen and to stretch during the middle part of nestling life. Preening commenced on days 8–9, shortly after the rupture of many teleoptiles, and it probably aided in the removal of sheaths during the latter part of the nestling period. Preening was initially directed toward the wing, under the wing, and to the breast, as in Song Sparrows (*Melospiza melodia*) and American Redstarts (*Setophaga ruticilla*) (Nice 1943). Stretching up of both wings was already present on day 5, and other stretching movements appeared on days 6–8. Stretching down of both wings, a temporary movement in passerine development (Nice 1943), occurred only on days 8–10.

The birds scratched their heads from day 12, just after fledging. At first they scratched directly, but soon they began to scratch indirectly as well. On day 16 and thereafter, they invariably used the indirect method. This ontogenetic pattern of direct scratching superseded by indirect scratching has been reported in several other passerines and in a few non-passerines (Ficken and Ficken 1958, Nice and Schantz 1959, Berger 1966).

The birds began to shake themselves shortly after fledging. They slept with their bills tucked into the upper wing coverts from the time of fledging,

Table 6

Percentage of Free-living, Young Brewer's Blackbirds Capable of Grasping and Balancing with Increasing Age

Age in Days	n	Behavioral Capacity[1]					
		DNG	G < 5	G ≥ 5	B < 5P	B ≥ 5F	B > 5G
3	15	100	0	0	0	0	0
4	21	71	29	0	0	0	0
5	19	32	47	21	0	0	0
6	14	0	36	64	0	0	0
7	20	0	0	90	10	0	0
8	16	0	0	31	69	0	0
9	15	0	0	20	53	20	7
10	11	0	0	0	0	36	64
11	9	0	0	0	0	0	100

[1] DNG = does not grasp; G < 5 = grasps < 5 sec; G ≥ 5 = grasps ≥ 5 sec; B < 5P = balances < 5 sec, coordination poor; B ≥ 5F = balances ≥ 5 sec, coordination fair; B > 5G = balances > 5 sec, coordination good.

but they did not support themselves on one leg on a perch until days 18–19. They performed bathing movements, always at water, beginning on days 18–23. Occasionally, they adopted a sunning posture near a lamp starting at 25–34 days.

Locomotion and related activities.—The first locomotor activity to develop was righting. Of 12, 0-day-old nestlings placed on their backs on a flat surface, 11 made no attempt to right themselves, and one squirmed slightly but could not turn over. On day 1, four of 10 birds placed on their backs righted themselves, five turned onto their sides, and one made no effort to turn over. On day 2, all of 10 birds righted themselves. Soon afterwards, nestlings began to raise themselves on their tarsi, at first only during gaping. They also began to crawl at this time.

The ability to grasp and balance developed gradually during the nestling period. At 3–5 days, birds began to cling to the nest lining with their toes during removal from their nests. Free-living nestlings failed to grasp a perch, 16 mm in circumference, placed against their feet on day 3 (Table 6). On day 4, six of 21 birds were able to grasp the perch weakly; and by day 6, nine of 14 birds grasped firmly for 5 sec. Most birds were first able to balance unsteadily on the perch on day 8, and to balance with good coordination on day 10.

Nestlings, both free-living and hand-raised, were consistently unable to balance when first able to grasp a perch. A similar phenomenon has been reported in seven species of terrestrial breeding, non-icterine passerines

(Holcomb 1966a). However, Holcomb (1966b) found that nestlings in an upland breeding population of Red-winged Blackbirds were usually able to balance when first able to grasp. He suggested that this early ability to balance was the product of strong selection pressure in an aquatic environment, on a species which has recently spread into terrestrial habitats. If this hypothesis is correct, one would suspect that an icterid historically nesting in terrestrial situations should fit the developmental pattern of terrestrial breeding non-icterids rather than that of the Red-winged Blackbird. My results indicate that the statement holds for Brewer's Blackbirds.

Fledging by free-living young occurred at the earliest between days 9 and 10, and at the latest on day 13. Williams (1952) found the nestling period at undisturbed Brewer's Blackbird nests to be 13 days. Disturbance was a contributing factor to early nest-leaving by some birds in my study. On a few occasions, young of 10–12 days fledged as I approached their nests. Birds from the age of 9 days were generally restless when I returned them to their nests after routinely examining them, but in several cases I was successful in preventing premature fledging by cupping my hands over a nest for several minutes until its occupants became calm.

Locomotion on the ground was initially by hopping, beginning on days 9–11 in free-living young. A variant of hopping was "hop-walking," in which hops were interspersed with walking steps. Both hopping and hop-walking were usually accompanied by fluttering of the wings. Several other passerines which walk as adults, have been reported to hop when they first leave the nest (Nice 1943, 1950; Horwich 1969). Another early form of terrestrial locomotion was walking on the tarsi, used over short distances. Walking in the adult manner appeared on day 13 at the earliest, and it entirely replaced other gaits in hand-raised birds by day 20.

Flying was preceded by fanning of the wings, beginning on day 9 in hand-raised nestlings. Free-living birds were capable of short (< 1 m) descending flights on days 10–11, at which time the wing chord was about 55% that of adults. One free-living, 13-day-old fledgling flew horizontally for approximately 5 m. Red-winged Blackbirds and Brown-headed Cowbirds (*Molothrus ater*) are also capable of some flight at the time of fledging (Nice 1950), but Yellow-headed Blackbirds (*Xanthocephalus xanthocephalus*) are unable to fly for the first 4–5 days after they leave the nest (Fautin 1941). Hand-raised Brewer's Blackbirds did not begin to fly until several days after fledging; however, I believe that this was at least partly due to insufficient motivation, since flight by free-living birds generally occurred during attempts to escape from me. Coordination upon landing was at first poor to fair in both free-living and hand-raised birds. Captives were able to land skilfully by day 23.

Escape responses.—Free-living young crouched when I approached their nests, beginning usually on days 7–8 when their eyes had opened to about 3 mm (16 of 20 birds). Of four hand-raised nestlings, only one gave this response to me, at 10 days. Schaller and Emlen (1961) found that free-living, nestling Common Grackles (*Quiscalus quiscula*) opened their eyes to 3 mm by 200 hours and began to crouch to a visual stimulus at 200–220 hours (days 8–9). These workers additionally demonstrated that pattern vision was acquired as early as 150 hours (day 6), and that visual experience was necessary for the normal development of discrimination between parent birds and other stimuli appearing at the nest rim. Further study might be expected to yield similar results for Brewer's Blackbirds.

Free-living nestlings aged 10 days or older occasionally hopped or fluttered from their nests at my approach. Fledglings aged 11–13 days typically crouched motionless until I touched or almost touched them, when they attempted to escape. Such responses to me were rare or absent in hand-raised birds up to the age of about 5 weeks. However, as the captive birds attained independence in feeding, they began to escape when I approached them.

Social behavior.—Hand-raised birds began to peck or nibble at one another's bill, toes, tail, and body feathers shortly after fledging. Such pecking evoked no discernible responses by recipients during the first several days out of the nest. Birds at this age occasionally begged to, and landed upon, one another.

Mutual pecking, followed by the retreat of one bird, occurred on day 25 and thereafter. Pecking encounters were usually precipitated when two birds attempted to gain possession of a single food item, such as an insect. On day 27, a bird at a feed dish faced an arriving bird and opened its bill, whereupon the newcomer retreated. This threat posture was assumed on many later occasions, usually in the presence of food. A threatened bird sometimes responded by assuming a similar posture: if neither bird retreated, the encounter either ended in a standoff or resulted in a fight. The largest bird, a male, was dominant to both females.

Vocalizations.—Free-living birds gave four calls which appeared in the following order: (1) peeping sounds, (2) "tutz-utz-utz," (3) the squawk, and (4) the location note (terminology after Williams 1952). Ten recently hatched nestlings gaped without vocalizing. However, day 0 nestlings older than 2-3 hours gave peeping sounds while gaping (Fig. 6). The call was produced in series and appeared to be associated with hunger. At 6–9 days, birds began to give a second, similarly motivated call of lower frequency, "tutz-utz-utz." This call appeared initially as a single note interspersed with peeps, but by days 10–12 it had replaced peeping sounds and was given in series.

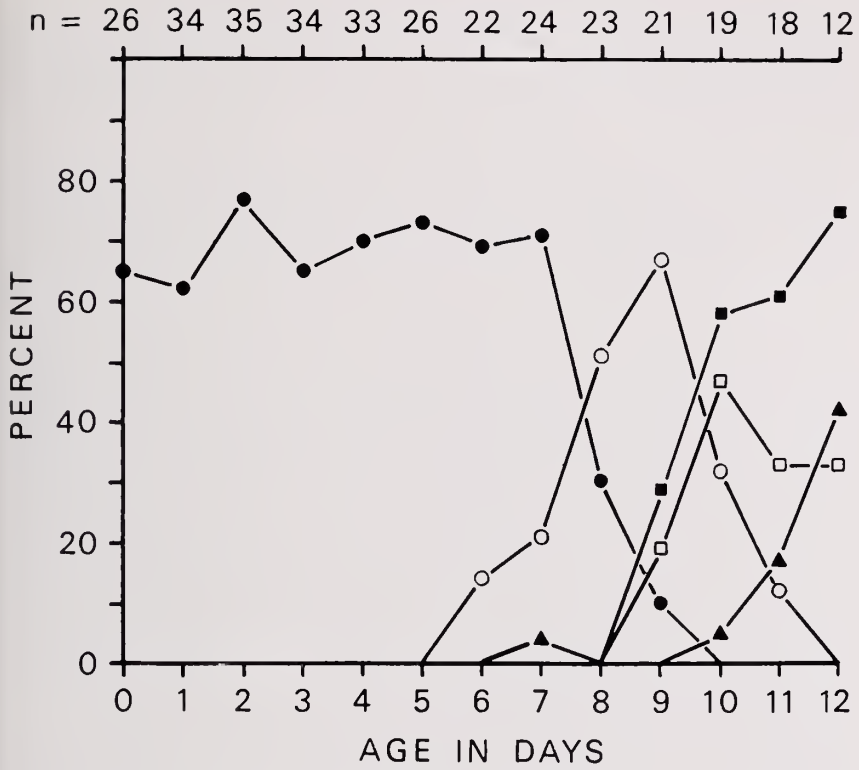


FIG. 6. Percentage of free-living, young Brewer's Blackbirds giving several calls with increasing age: (●) peeping sounds; (○) mixture of peeping sounds and "tutz-utz-utz;" (□) "tutz-utz-utz;" (▲) squawk; (■) "chup."

A third call, the squawk, was a single, harsh note of approximately 0.2 sec duration. Stimuli which evoked this call were capture of birds by me and sudden movement in the birds' immediate environment. I first heard the squawk on day 7, the age at which crouching appeared. A fourth call was a single, short, low frequency "chup." Williams' (1952) "location" note. Birds gave this call from the age of 9–10 days while standing or hopping on the ground, either as fledglings or as nestlings temporarily removed from their nests by me. "Chup" calls by one bird evoked similar calls from nearby siblings.

Hand-raised birds gave each of the above calls, in a sequence similar to that in free-living birds. The captive birds continued to give occasional peeping sounds for about a week after fledging, at times when they were partly satiated with food. The "peep" call in these fledglings appeared to function

as a low intensity begging vocalization, to be replaced by the louder, more conspicuous "tutz-utz-utz" as time since the last feeding increased. At 5–6 weeks, hand-raised birds sometimes gave squawks when subordinated during agonistic encounters. Williams (1952) reported squawks from adults under similar circumstances.

A hand-raised male gave subsong beginning at 28 days. A female produced subsong on one occasion, at 35 days. These observations of subsong are consistent with findings for other young passerines (Lanyon 1960).

SUMMARY

The purpose of this study was to describe the development of young Brewer's Blackbirds. Observations were made of morphology and behavior in 41 free-living nestlings aged 0–13 days, and of behavior in four hand-raised birds aged 5–42 days.

Recently hatched nestlings averaged 3.7 g or 6% of the weight of adult females. Daily weight gains increased until day 5, then decreased. By day 10, the birds averaged 70% of adult female weight. Within asynchronously hatched broods, last-hatched birds made smaller daily gains than did first-hatched birds.

The wing, the tarsus, and the hallux followed a sigmoidal growth pattern. By day 10, the tarsus was almost fully grown, whereas the wing chord was slightly over half of adult size. Growth of the commissure exceeded that of the culmen on days 1–4, then dropped below that of the culmen.

The nestlings were sparsely covered with whitish down at hatching. Sheaths of primaries emerged through the skin on day 2 and ruptured on day 6. Sheaths of teleoptiles in other regions emerged on days 3–7 and ruptured on days 6–10.

The nestlings' eyes began to open on days 1–3 and were fully open by days 8–9. Sexual dimorphism in eye color was faintly discernible at 12–13 days and was obvious in hand-raised young by 3 weeks. The nestlings had red mouth linings. Their bills, tarsi, feet, and claws were pale at hatching and were nearly black by the time of fledging.

The nestlings first gaped shortly after hatching. They began to orient their gaping at 7–9 days and to show independent feeding responses near the time of fledging. Hand-raised birds attained complete independence in feeding by 39 days. Nestlings and fledglings occasionally regurgitated pellets.

The birds began to preen and to stretch in the middle part of the nestling period. Hand-raised young scratched their heads from the age of 12 days, at first directly, later indirectly.

Nestlings were first able to right themselves on days 1–2. Most birds were able to grasp a perch for 5 sec on day 6, to balance unsteadily on day 8, and to balance with good coordination on day 10. They fledged on days 9–13, and they hopped before they walked. Free-living birds were capable of short (< 1 m) flights on days 10–11 and of longer flights by day 13.

Free-living nestlings began to crouch at my approach at 7–8 days. Hand-raised birds showed agonistic behavior, including pecking encounters and an open-billed threat posture, starting at 25–27 days. Birds aged 0–13 days gave two begging calls, a squawk, and a "location" note; and hand-raised young produced subsong beginning at 4–5 weeks.

ACKNOWLEDGMENTS

I wish to thank Kenneth L. Diem for his advice during the hand rearing phase of this research.

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DEPT. OF BIOLOGY AND THE ECOLOGY CENTER, UTAH STATE UNIV., LOGAN 84322. ACCEPTED 6 SEPT. 1974.

REQUEST FOR ASSISTANCE

Wood Storks.—As part of an intensive investigation of the biology of Wood Storks, nestling birds in several Florida rookeries are being color-marked. In 1974, red nasal saddles were placed on juvenile storks in south Florida, while in 1975 red patagial disks were used in south Florida rookeries, and blue patagial disks in central Florida. Any sightings of these color-marked storks, or anyone having knowledge of the location of recent Wood Stork nesting, please contact John C. Ogden, National Audubon Research Department, 115 Indian Mound Trail, Tavernier, FL 33070.

COMPARATIVE FEEDING BEHAVIOR OF THREE COEXISTING TYRANNID FLYCATCHERS

Nicolaas A. M. Verbeek

Flycatching, although occasionally practiced by numerous kinds of birds, is the main feeding method in many species of tyrannid flycatchers. Flycatching is not a stereotyped behavior. Instead, there is considerable diversity in the methods evolved by its practitioners. The object of this paper is to analyze some of the spatial and temporal aspects of flycatching and to present data on this and other ways in which competition among coexisting flycatchers might be reduced.

In theory, the less overlap in the use of available resources, the better it is for the individual species. The study of related sympatric species, such as flycatchers, is of particular interest, and could supply additional evidence in support of the competitive exclusion principle (Gibb 1951, MacArthur 1958, Lack 1971). Differences in habitat use among such species may involve many factors, including the type and size of food taken, foraging height, and feeding tactics. Comparative niche relationships among other species of flycatchers have been reported in several studies (Johnson 1963; Hespenheide 1964, 1971; Crowell 1968; Smith 1966; Johnston 1971; Williamson 1971).

STUDY AREA AND METHODS

This study was conducted at the Hastings Reservation, Monterey Co., California, where three species of small flycatchers (for measurements, see Table 1) coexist in riparian woodland: the Western Flycatcher (*Empidonax difficilis*), Western Wood Pewee (*Contopus sordidulus*), and the Black Phoebe (*Sayornis nigricans*). The Western Wood Pewee also occurs on slopes with scattered trees, and the Black Phoebe frequently ventures out into grassland along fences. The three species depend for 99% of their diet on invertebrates (Beal 1912).

Because of the small breeding population involved, collecting of stomach samples to study the diet of the various flycatchers was not feasible. Instead, I used differences in foraging behavior and feeding substrate to indicate differences in habitat exploitation. For each species I recorded the estimated height of its perch and the distance flown between the perch and the prey. I also noted whether a flight was ascending, horizontal, or descending. Two methods of catching prey were distinguished: hawking and gleaning. I define hawking as the capture of a flying insect. Gleaning means the capture of an insect sitting on any kind of substrate. Frequently a bird hovered in front of a sitting insect before taking it. Such hovering flights were classified as gleaning. Gleaning from the ground occurred after a bird landed nearby (Black Phoebe) or in a passing flight (Black Phoebe, Western Flycatcher).

For each feeding sortie I recorded whether the bird returned to the perch it flew from (return flight), or whether it flew to a new perch (no-return flight). A return flight is one where a bird returns to the exact perch it flew from or to a site within a

Table 1

Some Measurements and Weights of the Three Species of Flycatchers. Data from Ridgway (1907) unless otherwise indicated

Species	N	Wing (mm)	Tail (mm)	Tarsus (mm)	Culmen (mm)	Weight[1] (g)
Sayornis nigricans semiatra	14	90.6	78.9	17.8	15.2	19.0
Contopus sordidulus sordidulus	19	84.6	62.3	13.2	13.1	14.0
Empidonax difficilis difficilis	14	64.2	54.8	16.4	11.5	11.2

[1] N = 20 (10 males and 10 females). Courtesy of Ned K. Johnson.

few cm from the original one. As all three species perched in trees in varying degrees, I arbitrarily divided the tree into seven regions: an outer shell and an inner core, each of which was divided into a lower, middle, and upper layer, and the top (Fig. 1).

Feeding tactic diversity values were calculated using the formula $FTD = \Sigma_i P_i \ln P_i$, where P_i is the proportion of the species in question using the ith feeding tactic. The same formula was used to calculate substrate diversity (SD).

I recorded data throughout the day whenever one of the species was encountered: from 10 July to 8 August 1967 for the Black Phoebe, from 7 July to 11 August for the Western Wood Pewee, and from 7 July to 9 August for the Western Flycatcher. Because there were few birds, I put no restrictions on the number of observations and the length of time each bird was followed.

RESULTS

Nest site selection.—In selection of nest sites the Western Flycatcher and the Black Phoebe approached each other more closely than either species did to the Western Wood Pewee. One ledge under an overhanging roof was used by Black Phoebes in 1968, and by Western Flycatchers in 1969. Neither nest was completed, and there were no remains of the phoebe nest in 1969.

The study area contained three nests of the Black Phoebe, three of the Western Flycatcher, and at least one of the Western Wood Pewee. The territories of all three species partly overlapped. In 1969, a nest of the Black Phoebe, Western Flycatcher, and Western Kingbird (*Tyrannus verticalis*) were situated about 15 m from each other. The nest sites of Western Flycatchers on my study area were on the outside wall of a building at 1.5 m, inside a shed at 2 m, and inside a barn at 8 m. One Black Phoebe nest was on the outside wall of the same barn at 3 m, one under an overhanging roof at about 2 m, and another nest was inside a water tank at about 2.5 m. The only known nest of a Western Wood Pewee was located at about 9 m in a tree.

Egg dates.—At the Hastings Reservation, Black Phoebes normally have two clutches per year. From 1968 to 1970, first eggs in 10 early clutches appeared between 28 March and 23 April, and those of 10 second clutches

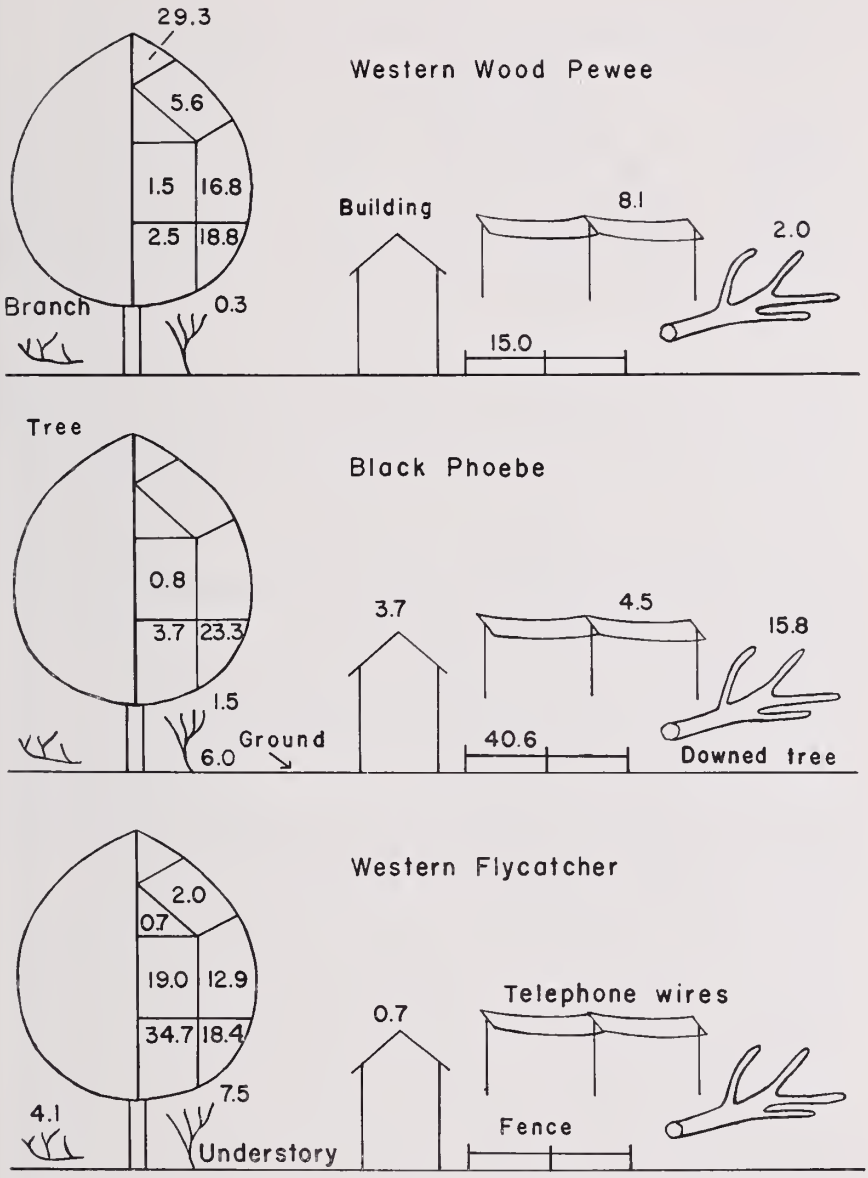

FIG. 1. Location of perches from which three species of flycatchers direct their feeding sorties, expressed as a percentage of all perches for each species.

Table 2

Estimated Height of Perch and Distance of Flight to capture Prey[1]

Species	N	Height of perch (m)			Distance of flight (m)		
		Median	Inter-quartile distance	Range	Median	Inter-quartile distance	Range
C. sordidulus	323	5.61	2.96–9.96	0.25–35	3.75	2.00–6.80	0.25–35
S. nigricans	133	1.16	0.78–2.63	0.75–10	2.04	1.21–4.58	0.25–15
E. difficilis	113	5.05	2.05–7.67	0.25–17	1.68	0.98–3.07	0.25– 8

[1] The frequency distributions of perch height and flight distance for all species were positively skewed.

between 17 May and 15 June. First clutches of four nesting Western Flycatchers were begun between 29 April and 2 May, and second clutches in two were between 25 June and 5 July. This is in agreement with data provided by Davis et al. (1963). I do not have information on the Western Wood Pewee.

Perch selection and flight distance.—The three species show clear differences in their preferred perches from which to hunt (Fig. 1). The Black Phoebe selected fences, the outer lower tree canopy, and fallen dead trees in meadows. It was the only one of the three species to perch on the ground to catch prey. About 30% of its perches were in trees. The Western Wood Pewee preferred exposed high perches, such as tree tops, the outer tree canopy, and telephone wires. Nearly 75% of its perches were in trees. The Western Flycatcher was almost entirely restricted to the middle and lower interior of trees, an area not used extensively by the other two species.

Substrate diversity indices, based on Fig. 1, in which all tree perches are lumped and treated as one, for the species were: Black Phoebe (1.51), Western Wood Pewee (0.81), and Western Flycatcher (0.48).

The median perch height of the Western Wood Pewee was not significantly different from that of the Western Flycatcher ($\chi^2 = 2.17$, $P > 0.05$, Median test in Siegel, 1956) (Table 2). These two species differed significantly ($P < 0.05$) in perch height from the Black Phoebe. Among the three species, perch height and flight distance to capture prey were not directly related.

The Western Wood Pewee flew the longest distance to capture prey (Table 3) and its median flight distance differed in this respect significantly ($P < 0.05$) from the Black Phoebe and the Western Flycatcher. The latter two did not differ significantly from each other in median flight distance ($P > 0.05$).

Foraging tactics.—All three species hawked predominantly (Table 3), and this was the only maneuver employed by the Western Wood Pewee. In

TABLE 3

FORAGING METHODS OF THREE SPECIES OF FLYCATCHERS, EXPRESSED AS A PERCENTAGE OF ALL FEEDING FLIGHTS FOR EACH SPECIES

Foraging method	*C. sordidulus* (N = 323)	*S. nigricans* (N = 133)	*E. difficilis* (N = 113)
Hawking			
in tree	3.7	0	15.0
under tree	0.3	0.8	0
among tree leaves	0.3	1.5	14.3
over grass	7.4	24.1	0.7
over ground	0	0.8	0.7
in open air[1]	87.0	49.6	29.3
Total	98.7	76.8	60.0
Gleaning			
from tree trunk	0	0	6.1
from stems, branches	0.3	0	11.6
from tree leaves	0.9	2.2	18.4
from ground	0	8.3	2.7
from grass	0	8.3	0
from buildings	0	4.5	1.4
Total	1.2	23.3	40.2

[1] Away from vegetation or ground.

contrast, the Western Flycatcher, largely confined to perching in the interior of trees, hawked slightly over half of the time. Hawking flights of the Western Wood Pewee were directed predominantly into the open air away from vegetation or the ground. The feeding tactic diversity values for the three species were: Black Phoebe (1.14), Western Wood Pewee (0.53), and Western Flycatcher (1.88). In all species returns to another perch occurred significantly more often than returns to the original perch (Table 4). This was particularly noticeable in the Western Flycatcher.

As length of flight and tendency to return to the same perch are related in the Eastern Kingbird (*Tyrannus tyrannus*) (Leck 1971), I analyzed this relationship in the three species I studied. In contrast to the Eastern Kingbird, the three species showed a unimodal distribution of flight lengths, strongly skewed toward shorter lengths. The means of the distributions lie so close to zero-flight-distance that it is meaningless to determine the relationship of short flights and return or no-return to the original perch. However, this relationship or the lack of it can be shown for long flights. To determine long flights I started at the longest flight length in each of the three frequency distributions, counting inward until I had one quarter (or

Table 4

Tendency to Return to Original Perch by Three Species of Flycatchers

	Return to original perch								
	All flights				Long flights only				
Species	N	Yes %	No %	χ^2	Distance (m)	N	Yes %	No %	χ^2
C. sordidulus	323	38.1	61.9	18.36[1]	≧ 8	75	38.6	61.4	3.85
S. nigricans	133	23.3	76.7	37.90	≧ 5	33	27.0	73.0	6.81
E. difficilis	113	2.7	97.3	101.32	≧ 4	22	0.0	100.0	22.00

[1] Critical χ^2 ($P \leq 0.05$) ≧ 3.84.

less if inclusion of the next frequency brought the total over a quarter of all entries). No-return flights predominated significantly (Table 4). Considering long flights, comparison of the frequency of return and no-return flights between the Western Wood Pewee and the Black Phoebe was not significantly different ($\chi^2 = 0.85$, $P > 0.3$). The comparison between the Western Wood Pewee and the Western Flycatcher and between the latter and the Black Phoebe was significantly different ($P < 0.001$, and $P < 0.02$ respectively). I used the same procedure to assess high and low perches: again, no-return flights occurred significantly more often than return flights, regardless of perch height (Table 5). The Western Wood Pewee and the Black Phoebe do not differ significantly in the frequency of return and no-return flights from high perches ($\chi^2 = 2.19$, $P < 0.10$). Both species differ significantly in this respect from the Western Flycatcher ($P < 0.001$, and $P < 0.05$ respectively). Comparing low perches, the Western Wood Pewee differs significantly in the frequency of return and no-return flights from the Black Phoebe ($P < 0.05$) and from the Western Flycatcher ($P < 0.01$). The

Table 5

Comparison between High and Low Perches and Return (R) and No-return (NR) Flights to the Original Perch

	High perch					Low perch				
Species	Height (m)	N	R %	NR %	χ^2	Height (m)	N	R %	NR %	χ^2
C. sordidulus	≧ 11.0	76	36.8	63.2	5.26[1]	≦ 2.5	74	36.5	63.5	5.41
S. nigricans	≧ 3.5	26	19.2	80.8	9.84	≦ 0.5	29	13.8	86.2	15.21
E. difficilis	≧ 8.0	32	0.0	100.0	32.00	≦ 1.5	22	4.5	95.5	18.18

[1] Critical χ^2 ($P \leq 0.05$) ≧ 3.84.

TABLE 6

DIRECTION OF ALL FEEDING FLIGHTS, AND RELATIONSHIP BETWEEN FLIGHT LENGTH AND PERCH HEIGHT AND DESCENDING (D), HORIZONTAL (H), AND ASCENDING (A) FLIGHTS IN THREE SPECIES OF FLYCATCHERS

	Direction of all feeding flights					Long flights				Short flights			
Species	N	A %	H %	D %	$(\chi^2)^1$	N	A %	H %	D %	N	A %	H %	D %
C. sordidulus	323	32	17	51	13.44	75	67	17	16	76	55	22	22
S. nigricans	133	30	27	43	2.98	33	46	15	39	26	42	19	39
E. difficilis	113	47	24	29	4.66	22	41	27	32	32	25	28	77

[1] Chi square values based on ascending and descending flights only ($\chi^2 \geq 3.84$, $P \leq 0.05$).

Western Flycatcher and the Black Phoebe do not differ significantly in this respect ($\chi^2 = 0.39$, $P < 0.50$). As expected, high perches, in contrast to low ones, were associated with long flights; i.e. in *C. sordidulus* (26 high perches versus 5 low ones), in *S. nigricans* (9 and 0 [zero]), and in *E. difficilis* (7 and 3 respectively).

For each foraging flight I noted whether the birds flew upward, horizontally, or downward from the perch in pursuit of prey. All three species differed significantly in the distribution of their flight directions (pewee versus phoebe $\chi^2 = 6.10$, $P < 0.05$: pewee versus Western Flycatcher $\chi^2 = 15.75$, $P < 0.001$; phoebe versus Western Flycatcher $\chi^2 = 7.92$, $P < 0.02$). The Western Wood Pewee had significantly more descending flights than ascending flights. In the Western Flycatcher ascending flights significantly predominated, while these two flight directions did not significantly differ in the Black Phoebe (Table 6). In the Western Wood Pewee, descending flights tend to be long ones and they are associated with high perches (Table 6).

Interactions.—I saw interspecific interactions between the Black Phoebe and the Western Wood Pewee only twice. These encounters occurred in the outer lower tree canopy. In both cases the Black Phoebe was dominant. Several times these two species sat near each other on a fence wire without interacting. I saw no hostility between the Black Phoebe and the Western Flycatcher. Only once did a Western Flycatcher chase a Western Wood Pewee.

DISCUSSION

Although there must be some overlap in insect species taken, differences in the methods of feeding and preferred perch sites may be factors acting to lessen any competition between these flycatchers.

The Western Wood Pewee prefers exposed high perches on the outside of trees, it flies the longest distance, and primarily hawks by diving on its prey in the open air away from vegetation. It is the fastest flier of the three species. At the other end of the scale, the Western Flycatcher hunts in the interior of trees, where its view and path of flight is hindered by branches, hence its short flight distance. The many branches and leaves provide perches for insects, which explains the large proportion of gleaning noted for this species. The Western Flycatcher flies in quick darts and has the widest range of foraging tactics. The Black Phoebe stays close to the ground and is found primarily in the open, where it feeds by hawking over vegetation and in the open air.

The Black Phoebe shows the widest diversity of the three species in its use of different substrates, but it is intermediate in its diversity of feeding methods. Although the Western Flycatcher has a greater diversity of feeding methods than the Black Phoebe and the Western Wood Pewee, it has a very narrow substrate diversity. Of the three species the Black Phoebe appears the most versatile.

No-return flights significantly outnumbered return flights, and this was neither related to flight length, nor to perch height. Leck (1971) suggests that return flights may be associated with high prey density, in the absence of which a flycatcher might have to search and move from perch to perch. He also suggests that long flights tend to be associated with large prey items, while short flights involve small prey. Regarding the first point, frequent returns to the same perch in situations of insect abundance may not apply in flycatchers such as the Western Flycatcher, which hunt over small distances, as frequent sallies disturb the prey near the perch. Concerning the second point, I could not see the size of the insects that were caught, but it seems reasonable to expect that at larger distances proportionally more large insects are sighted than small ones. However, large insects tend to struggle when caught and preferably need to be dealt with on the nearest perch rather than the original one. I suggest that flight distance is probably not so important in determining whether a flycatcher does or does not return to its perch.

In any case, the association between long flights and no-returns is not supported by my own data nor by Leck's (1971) remarks concerning the Olive-sided Flycatcher (*Nuttallornis borealis*). A simpler explanation that applies to all five species discussed here, lies in the availability of alternative perches, to which Leck alluded, and to the species' choice of perch sites. The Western Flycatcher, inside the canopy, has plenty of perches to choose from. The Black Phoebe and the Eastern Kingbird live in the open in a habitat with ample fence rows and weed stalks. Here again, return to the perch is not necessary as others are available, but the choice is more limited

than in the case of the Western Flycatcher. Lastly, the Western Wood Pewee and the Olive-sided Flycatcher use high, preferably bare perches in tree tops, and these are in limited supply.

Natural nest sites of the Black Phoebe, such as rock faces, have been greatly augmented by the vertical walls of buildings and bridges. The Western Flycatcher also uses buildings, but it needs a more or less horizontal surface on which to construct its nest. These are usually available inside and, to a lesser degree, outside buildings. Western Flycatchers also nest occasionally on ledges, and Davis et al. (1963) report one nesting above water. Along streams, where both find optimum habitat, as well as on buildings, the two species thus show potential and in some cases actual overlap in nest site selection. As nest height and foraging height in the two appear related (see also Johnston 1971), the overlap in requirements may be lessened in that their nesting cycles are neatly out of phase (pers. obs.). When the Black Phoebe has its first brood the Western Flycatcher is just beginning to lay its first clutch. This is repeated in the second brood. The periods when the young of both species are in the nest, and during which they require most food, thus do not overlap.

For eastern forests Hespenheide (1971) concludes that not more than one species of small flycatcher, such as the Eastern Wood Pewee (*Contopus virens*), coexists with the large Crested Flycatcher (*Myiarchus crinitus*). In contrast, Johnston (1971) reports overlapping territories among *M. crinitus*, *C. virens*, and *Empidonax minimus*, and among *M. crinitus*, *E. minimus*, and *Sayornis phoebe*. This apparent discrepancy probably results because Hespenheide's study was based on flycatchers living in undisturbed habitats, while Johnston apparently worked in a disturbed area rich in ecotones. The overlap among the three small species in my study is likely due to similar reasons. The broken pattern of vegetation probably provided a greater variety and abundance of insects. Johnston (1971) noted no evident conflicts among these four species, as is the case in my study with the three exceptions mentioned. The generally aggressive nature of the Western Flycatcher is reported by Williams (1942) and Davis et al. (1963), and its attack on the Western Wood Pewee may be part of that syndrome. The lack of aggression among the three species, especially between the Black Phoebe and the Western Flycatcher, suggests that their niches are well adjusted to each other.

SUMMARY

During the breeding season the territories of the Black Phoebe, Western Wood Pewee, and Western Flycatcher overlapped, and the species showed little sign of interspecific aggression. Potential competition among these flycatchers appears to be reduced by

interspecific differences in nest site selection, nest height, breeding season, foraging tactics, and the choice of perch sites. It is suggested that the Black Phoebe is the most versatile of the three species, and it is the only one to feed on the ground.

ACKNOWLEDGMENTS

The data presented here were obtained incidental to studies supported by a grant from the Chapman Memorial Fund, American Museum of Natural History. I thank Mike Cullen, John Davis, Henry Hespenheide, Hans Kruuk, and my wife for commenting on an earlier version of this paper.

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MUSEUM OF VERTEBRATE ZOOLOGY, UNIV. OF CALIFORNIA, BERKELEY 94720 (PRESENT ADDRESS: DEPT. OF ZOOLOGY, ANIMAL BEHAVIOUR RESEARCH GROUP, SOUTH PARKS ROAD, OXFORD, OX1 3PS, ENGLAND). ACCEPTED 27 SEPT. 1974.

A WINTER POPULATION STUDY OF THE AMERICAN KESTREL IN CENTRAL OHIO

G. Scott Mills

Although considerable literature on the American Kestrel (*Falco sparverius*) exists, few studies on the dynamics of populations have been done. Raptor population studies are usually of a census nature, and data on movements and activities of individual birds are often limited. Enderson (1960) marked individual kestrels and monitored the dynamics of an Illinois population in spring and summer months. I followed a sizeable winter population from late October to early April with a high proportion of the population individually marked.

This study was conducted in an area of about 52 km^2 in south-central Ohio in the vicinity of the Ross-Pickaway County-line Road approximately 11 km south of Circleville. The area is north of the edge of glaciation in Ohio and is characterized by gently rolling hills and intensive agricultural use. Little woodland is present although scattered trees, especially in fencerows, are numerous.

METHODS AND MATERIALS

Kestrels were observed and marked during the winters from January 1970 to April 1972. A 72 km circuit was driven on most visits to the study area but was not always completed. Variations also occurred in time of day, time taken to complete the trip and number of observers. Five birds were trapped, transported, and released in the territories of others.

Trapping was done using the bal-chatri trap similar to that described by Berger and Mueller (1959) and birds were marked with wing tags similar to those used on gulls by Southern (1971). Modifications of Southern's technique included the use of strips that extended beyond the secondaries for better visibility and the attachment of an oval to the strip. By using ovals and strips in various color combinations, alternating wings, and taking advantage of the sexual dimorphism of kestrels, a large number of individuals could be uniquely marked.

Tags were both visible and durable. No tags were known to have been lost. Other than an initial period of attempting to rid themselves of the tags, kestrels showed no marked changes in behavior. Tags appeared not to interfere with normal activities, as tagged birds were seen hovering, capturing prey, and nesting.

RESULTS

Territoriality.—I observed territorial behavior when 4 of 5 kestrels were immediately chased when experimentally released within sight of other kestrels. Two females were released in male territories, one female was released in another female's territory, and a male was released in a female's

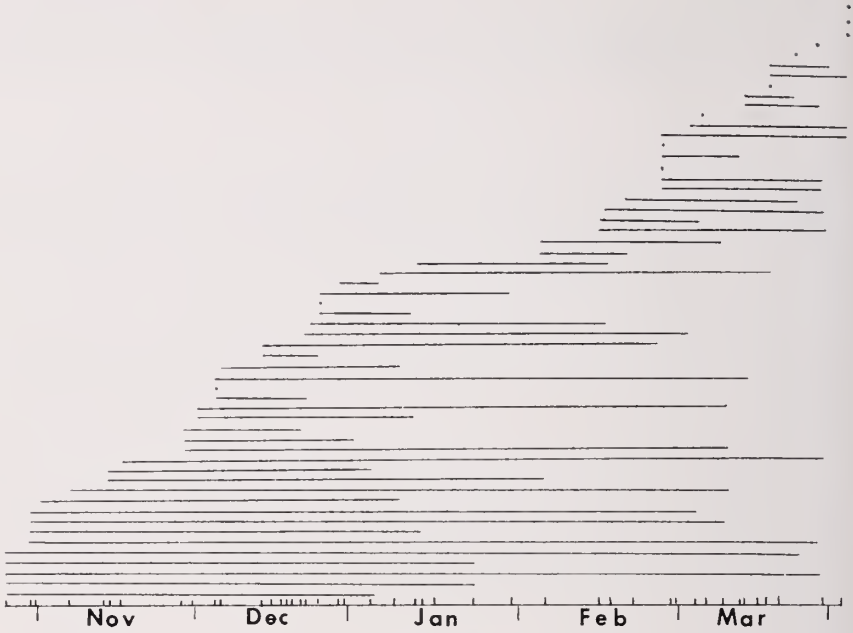

FIG. 1. Lengths of observation of individual kestrels, 1971–72. Tick marks indicate the date of a trip taken to the study area.

territory. In the fifth case a female released in the sight of a male eating a mouse was not chased. I observed unstaged fights between kestrels 3 times. In all encounters physical contact was observed only twice. Once a female drove a released male to the ground and pounced on it with outstretched talons several times. In the other case, involving 2 females at the edges of their territories, both birds fell to the ground several times while grappling. In all cases, it appeared that movement of the intruding bird was necessary to release aggressive behavior. Cade (1955) has also reported intraspecific winter territoriality in kestrels. In my study, territories were apparently defended against other raptors. Seven times kestrels were seen chasing Red-tailed Hawks (*Buteo jamaicensis*), once a Sharp-shinned Hawk (*Accipter striatus*) and once a Merlin (*Falco columbarius*).

I observed some overlap of territories but the only case in which I saw 2 kestrels in the overlapping portion of the territories was when 2 females were fighting. In at least 5 cases a male and female kestrel appeared to share a territory. These pairs were often seen perched near each other and it seemed that they attempted to stay together although one member of a pair was sometimes seen alone.

An important territorial requirement appeared to be the availability of a roost. I saw kestrels entering old buildings or barns 7 times and a hollow tree once at dusk. Every territory had at least one old or unoccupied building.

I estimated territory size by connecting extreme points of observation. For 16 tagged birds seen at least 5 times each, the average diameter of the territory was 1.4 km with the largest being 2.4 km. These territorial diameters are smaller than the diameters of the winter "ranges" of 1.5 miles (2.4 km) and 2.2 miles (3.5 km) reported by Enderson (1960) in Illinois and the Craigheads (1956) in Michigan, respectively.

Homing.—All 4 females, caught in late February or early March, were released 1.6 to 4.8 km from where they had been trapped and flew immediately in the direction from which they had come. Two were seen again where they had been caught: 2 were not seen again. A male brought into the area in late November from 24 km north was observed near the point of release over one month later.

Population changes.—Of interest was the inconsistent number of marked kestrels observed the winter after they had been tagged. Of 7 birds marked in early 1970, I saw 3 the following winter, but of 14 marked in the winter of 1970–71 I saw only one the next winter. In each case the birds were resighted where marked the previous year.

Figure 1 records the observations of individual kestrels in the winter of 1971–72. I made 44 trips to the area in 162 days. The extreme dates of observation of an individual were connected and I assumed that the bird remained in the area during the entire interval. The mean number of sightings of each kestrel was once every 2.5 trips to the area. Birds seen only once or twice on the periphery of the area were not included since an accurate sample of observations was unlikely. Of the 57 kestrels included, 39 were tagged, though not necessarily for the duration of the observation period. I feel that the consistency in location shown by tagged birds along with plumage and behavior differences allowed reliable identification of the untagged birds.

From Fig. 1 a graph of an estimate of the number of birds in the area at any particular time can be made (Fig. 2). The maximum population size was 27 on 24 December and the minimum was 17 on 30 January. Either number in 52 km^2 represents a much higher density than winter populations of 4 to 10 kestrels in 111 km^2 and 5 in 96 km^2 observed by Enderson (1960) in Illinois and the Craigheads (1956) in Michigan, respectively. Two peaks in population size occurred, resulting in 3 distinct periods which I will consider separately.

The population during the first period, 25 October to 24 December, steadily increased perhaps due to increased sampling. However, an actual

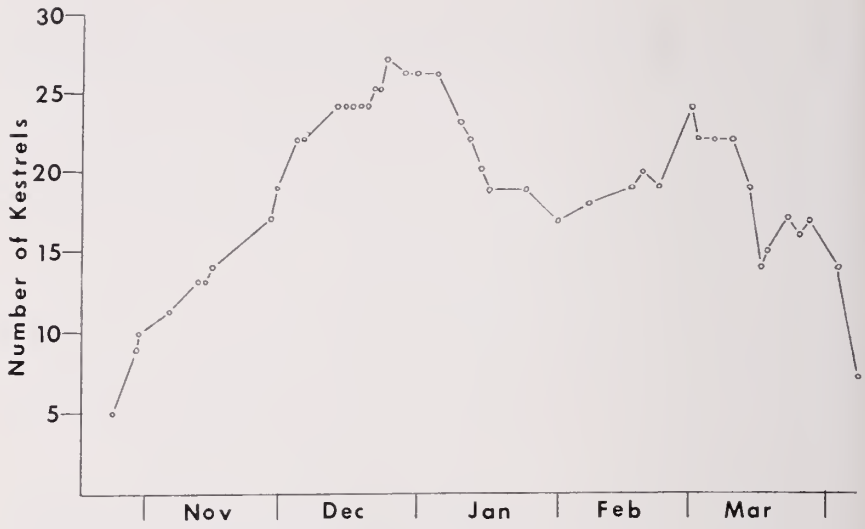

FIG. 2. Changes in population size of kestrels during the winter of 1971–72.

increase in population size is indicated. Several birds which first appeared in December were later observed regularly. For example, one female first observed 13 December after I had made 12 visits to the area was seen on 5 of the next 7 visits. The population during this period was quite stable. "New" birds appeared only in areas where none had been seen and only 3 were "lost."

The second period, 25 December to 30 January, was characterized by a rapid drop in population. Eleven of the birds from the first period were lost and only 3 were added. This period coincided with the first cold spell of the year in central Ohio with temperatures below −7°C and over a week of snow-covered ground.

The third period, 5 February to 4 April, was characterized by a population increase but losses were also high. Most new kestrels appeared in areas where others had been. The decline in March is difficult to analyze due to the termination of the study. It is interesting to note that the increase in the third period corresponds to the time of rapid population increase observed by Enderson (1960) in Illinois.

Another method of analyzing the population is by following segments of the population based on the month of the first sighting of each bird. The number of kestrels first seen in any one month that were also seen in subsequent months is recorded in Table 1. Of the 19 birds first seen in October or November, 9 (47%) were observed in March but of the 12 first observed in December only 2 (17%) were seen in March.

TABLE 1

LOSSES OF SEGMENTS OF THE KESTREL POPULATION BASED ON THE MONTH FIRST SEEN

First seen:	Number left in					
	Oct	Nov	Dec	Jan	Feb	Mar
Oct	10(8–2)*	10(8–2)	10(8–2)	10(8–2)	5(4–1)	5(4–1)
Nov		9(6–3)	9(6–3)	7(4–3)	5(3–2)	4(3–1)
Dec			12(7–5)	8(5–3)	4(3–1)	2(1–1)
Jan				2(2–0)	2(2–0)	1(1–0)
Feb					12(6–6)	9(3–6)
Mar						9(6–3)
Total	10(8–2)	19(14–5)	31(21–10)	27(19–8)	29(19–10)	30(18–12)

* (female–male)

Since individuals could be identified, sex ratios could be figured 2 ways: by the individuals present at any one time (from Fig. 1) or by the total sightings during a given time period (Table 2). Thus, a bird seen 4 times in a month constituted 4 sightings but only one individual. Although no significant difference ($\chi^2 = 0.27$, $p > .5$) between the 2 methods is observed, there does seem to be a bias for sightings of females, especially in January. For the entire winter, females averaged 5.6 sightings per bird and males averaged 4.8 sightings per bird.

Regardless of the method used, the percentage of males was lowest in October and November and gradually increased. Most of the imbalance is a result of the birds seen in October and November. During most of the study females outnumbered males by more than 2 to 1. Sex ratios of kestrel populations reported by other authors have been unbalanced but with a higher percentage of males in most cases (see Heintzelman and Nagy 1968).

DISCUSSION

The American Kestrel is listed as a permanent resident in Ohio by Borror (1950). The term "permanent resident" has a double meaning, being used in many state checklists for a species with any members present throughout the year but more properly defined as a "species not undergoing a regular periodical migration and consequently staying in one area the year round" (Pettingill 1970). In many cases the confusion of these definitions does not allow an adequate description of the true nature of many populations. My study indicates a heterogenous and changing population with little "permanency."

That some of the population were true permanent residents is indicated by those birds that were seen in the area the year after they had been tagged.

Table 2

Two Methods for Calculating Sex-ratios of Kestrels, Winter 1971–72

Month	By sightings			By individuals		
	♀	♂	♀:♂	♀	♂	♀:♂
October	8	4	2.0:1	8	2	4.0:1
November	21	7	3.0:1	14	5	2.8:1
December	66	31	2.1:1	21	10	2.1:1
January	33	6	5.5:1	19	8	2.4:1
February	35	10	3.5:1	19	10	1.9:1
March	40	28	1.4:1	18	12	1.5:1
Total year	203	86	2.4:1	36	18	2.0:1

Although almost no summer study was done, one female was known to have nested a summer between observations. Another indication of permanency was the relatively high percentage of kestrels first seen in October and November that were later observed in March.

Some birds seen were undoubtedly migrants, though few birds were seen only one time, possibly indicating a slow migration. That few kestrels first seen in December remained in March may reflect this. A major problem is that the disappearance of a bird may have been due to either migration or mortality.

The correlation of a period of cold and snow with the rapid drop in population suggests weather is an important factor influencing kestrel populations. Snow cover, especially, may reduce the hunting efficiency of kestrels preying on mice, which I observed to be the major prey during this study. Enderson (1960) reported that kestrels were less conspicuous on cold, windy days in Illinois; I noted this also. The difference in population density between this area and that of Enderson (1960) in Illinois and the Craigheads (1956) in Michigan is perhaps due, in part, to weather differences. Another factor may be differences in prey populations, although all are areas of fertile agricultural land. The smaller territory size found may reflect differences in food availability. Attempts to estimate small mammal populations were unsuccessful. Availability of roost sites may also be an important factor affecting population density. Areas that are very open with few buildings or tree hollows for roosts may not be suitable in colder climates.

The comparison of the 2 methods of calculating sex ratios indicates that sightings are an adequate way to sample sex ratios of kestrels. The sex ratio obtained in this study adds to the number of unbalanced populations of kestrels reported in the literature. Although I observed no difference in

territory between males and females, the sex ratio is consistent with the differential habitat selection shown by wintering kestrels in northern California (Koplin 1973). I have other data indicating this differential habitat selection is widespread.

SUMMARY

Individually marked American Kestrels studied in central Ohio showed definite winter territoriality. Winter population density was much higher and territory size was smaller than in similar studies done in Illinois and Michigan. Presence of a roost may be an important part of a territory. The population was quite dynamic, peaking in late December, dropping to a low in late January which correlated with cold weather and snow, and peaking again in February. During most of the study females outnumbered males by more than 2 to 1.

ACKNOWLEDGMENTS

I wish to thank the following persons who contributed to this study: E. E. Good and T. A. Bookhout for advice and help in administrative matters, Howard "Mac" Albin and Clive Petrovic for help in initial aspects of the study, Jim Silliman for reviewing the manuscript, and my wife, Liz, for much assistance throughout. Special thanks goes to W. E. Southern for providing initial ideas for the marking technique.

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BEHAVIORAL ASPECTS OF THE PAIR BOND IN WILSON'S PHALAROPE

Marshall A. Howe

Sex role reversal, in which females take the active role in pair formation and the smaller and more cryptically colored males take sole responsibility for incubation and parental care, is typical of all species of phalaropes (Bent 1927, Tinbergen 1935, Höhn 1965, 1967, Bengtson 1968, Hilden and Vuolanto 1972). In at least one species, the Northern Phalarope (*Phalaropus lobatus*), sex role reversal occurs in conjunction with serial polyandry, a system in which females form short-term pair bonds with at least 2 successive males (Raner 1972, Hilden and Vuolanto 1972). The behavioral mechanisms which enable species with sex role reversal to achieve effective integration of male and female roles, leading to formation of a pair bond and successful breeding, have not been examined in detail.

Howe (1975) discussed the social phase of early pair formation in flocks of Wilson's Phalaropes (*Phalaropus tricolor*) in North Dakota. The social phase takes place during the last week of April and the first half of May. At this time the birds confine most activity to open water of ponds and lakes and to segments of shoreline unobstructed by vegetation. Aggression among females competing for males manifests itself in both overt and ritualized form in swimming groups and during aerial pursuits. One immediate result of these interactions in both contexts is a reduction of competition among females for mates, either by increasing interfemale distances or by decreasing the number of females present.

Reduced competition among females leads to greater opportunity for direct interaction between a female and her potential mate. During the early stages of pair formation such interactions consist primarily of persistent attention and cautious approach by the female and occasional threat by the male. The female also performs an epigamic display, "Chugging," which often elicits male threat. As the male of a forming pair becomes more tolerant of the courting female, the birds spend more time apart from conspecifics and new behavior patterns begin to emerge. The present paper deals with this phase of pair formation in Wilson's Phalarope and examines the roles of the sexes in the pair bond. This period includes investigation of potential nesting areas, territoriality, nest-building, copulatory behavior, egg-laying, and certain other behavior patterns restricted to paired birds. The behavior of females after laying and its implications are also considered.

STUDY AREA AND METHODS

The observations reported here were made in May and June of 1969 and 1970 and in May of 1971 near Woodworth, Stutsman Co., North Dakota. The area, described in more detail elsewhere (Howe 1975), consists of rolling, highly disturbed, mixed-grass prairie with numerous small potholes of glacial origin. Phalaropes use the potholes for feeding and nest on the ground on the periphery of the potholes or on nearby higher ground. Most behavior observations were made in an area of approximately 1 km^2 which supported an average nesting population of 7 males.

Phalaropes were usually watched from an automobile or conventional portable blind. Durations of behavioral events were determined by stopwatch and, in certain cases, by recording the playback time of taped field notes. Most observations of behavior before egg-laying were made on unmarked birds. Three females and 2 males, however, were trapped during the egg-laying period with a spring-loaded bale trap anchored at the edge of the nest. These birds were marked with colored leg bands and diagnostic dye patterns on the plumage and released immediately.

Ten females were collected and examined for evidence of post-ovulatory follicles. In addition to gross examination, all ovaries were fixed, sectioned at 1 mm intervals, and stained, following the staining technique of Erpino (1969). This method of locating post-ovulatory follicles has been used successfully by Payne (1966) and Parmelee and Payne (1973).

In this paper the names of vocaliations and other behavior patterns which appear to be ritualized are capitalized, e.g. Pre-Copulatory Bow.

INVESTIGATION OF NESTING AREAS

By the third week of May most activity of courting groups of phalaropes had shifted from the central portions of large bodies of water to shallow water near shore and to smaller sloughs in which new growth of sedge (*Carex* spp.) was beginning to emerge. Although this was the peak period of aerial chasing activity, males were now better able to elude pursuing females by landing in vegetated sloughs and swimming into the vegetation. In such areas forming pairs were able to avoid detection by conspecifics for longer periods of time. In the absence of interference from other birds, potential mates began investigating drier grassy areas where nests would ultimately be placed.

Early ventures into grassy areas were nearly always initiated by the female (Table 1a). In about half of my observations the male did not follow and the female returned to the shore. Six cases in which unpaired females attempted to lead known paired males away from the shore elicited either threat by the male or no response at all.

When either a male or female left the shore and entered the grass the "crouch walk" posture was generally used (Fig. 1a). In this posture the neck was withdrawn, the body was tilted forward with the head slightly below the level of the tips of the wings and tail, and the back feathers were sometimes ruffled. Crouch-walking reduced a bird's conspicuousness in the grass and,

FIG. 1. Postures and displays associated with nest-area exploration, nest-construction and copulation: (a) Crouch-walk; (b) Pre-Copulatory Bow (PCB) Type I, also Scraping; (c) PCB Type II, also Ground-Pecking; (d) PCB Type III; (e) Pre-Copulatory Upright (PCU).

since the head was close to the ground surface, it probably facilitated close examination of potential nest locations. The position of the tail exposed the white undertail coverts to the following bird and may have been of significance in eliciting a following response.

The behavior of females after entering the grass could not be seen in many instances. Several times, however, I observed females adopt a form of the "Pre-Copulatory Bow" (PCB) posture (Fig. 1b, c, d) about 3 to 6 m from the shore. If the male was not already following the female, he usually ran toward her while she was performing the display, possibly in response to a vocalization rather than the posture per se. Sometimes this response led to fragmentary pre-copulatory behavior by both birds and at other times it led to nest-site searching. Copulatory and nest-site searching tendencies were

TABLE 1

MALE-FEMALE INTERACTIONS DURING THE PERIOD OF NEST-SITE SEARCHING

A. Relative positions while Crouch-Walking

	Sex Initiating Sequence	Sex Leading During Sequence
Female	27[1]	28
Male	3	30

B. Role in scrape ceremonies

Female Only	Male Only	Female Followed by Male	Male Followed by Female
15[1]	21	8	8

[1] Number of observations

occasionally expressed ambivalently. As a result it was often difficult to interpret the motivational basis of the behavior in these situations. Predominance of copulatory tendency was apparent in females which entered the grass with the neck extended vertically, a posture suggesting the "Pre-Copulatory Upright" (PCU) display (Fig. 1e). The complicated relationships between precopulatory and nest-site searching behavior are discussed further under "Copulatory Behavior."

Most early expressions of nest-site searching behavior that I observed began with a female and male walking out into the grass from a slough. Sometimes 2 birds would fly from a slough and land in dry grass some distance from the water, but these birds may have been ones which had already selected a potential nesting area. In mid-May old grass was generally less than 12 cm high in the areas selected except in occasional clumps. Early nesters began nest-site searching before new grass had emerged. Typically the 2 moved through the grass in the crouch-walk posture, one following the other or both wandering in separate directions and eventually rejoining. Usually visual contact was maintained but vocal communication also played an important role. Much of nest-site searching in this species was difficult to observe because the birds were often concealed by grass: but the instances observed (Table 1a) show that either sex may play a leading role once both are away from the shoreline.

Periodically during crouch-walking sequences, one sex or the other crouched in the grass and performed "Scraping" behavior. In this posture the bill was directed forward and down, the tail was raised almost vertically, and the tarsi were pushed backward against the wall of the shallow depression (or "scrape") that was formed (Fig. 1b). Sometimes the performing bird turned

around slowly in the depression. This was the same behavior performed later by males to form the cup at the nest, but at this early stage of the nesting cycle it appeared to be ritualized. It usually lasted for a few seconds and then the bird continued in a crouch-walk. Often the second member of the pair approached the Scraping bird from the rear and bowed forward in a posture similar to the first. This sometimes was followed by "Ground-Pecking," a display in which one or both birds pecked sporadically at the ground or grass in a stereotyped posture (Fig. 1c) similar to that of an uncommon form of the PCB. At this point the first bird may leave the depression while the second enters and Scrapes. Ritualized Scraping during pair formation was first given the name "Scrape Ceremony" by Huxley and Montague (1926), who observed it in the Black-tailed Godwit (*Limosa limosa*). Scrape Ceremonies have been reported for many ground-nesting birds particularly in the Charadrii and Laridae, occurring either in nest-site selection or precopulatory situations. Tinbergen's (1935) detailed account for the Northern Phalarope agrees closely with my observations of Wilson's Phalarope.

Although Scrape Ceremonies involved ritualized behavior patterns, the sequence of events was variable. Scraping by one bird did not necessarily elicit Scraping by the other, and often one sex Scraped while the other was too distant to observe. Often simultaneous Scraping by both occurred without Ground-Pecking. In one instance 2 birds Scraped simultaneously in the same spot while facing each other: then the female left and the male remained and turned slowly in the scrape for 10 sec after which the female returned and entered the scrape again.

Ground-Pecking often occurred when one sex replaced the other at a scrape. It was usually directed into the scrape itself and might be performed by both birds at the same time, closely resembling the "Egg Ceremony" of the Northern Phalarope (Tinbergen 1935). The performance of Ground-Pecking along with a Scrape Ceremony may be a mechanism for designating the most favorable potential nest locations. Ultimately the male alone denudes several scrapes by pulling up grass and rootlets. One of these scrapes becomes the nest, but the means by which the actual site is selected is not clear. A series of Scrape Ceremonies may last 2 hours or more at dozens of sites and cover distances up to 100 m.

Fifty-two instances of Scraping were noted (Table 1b). Either sex was equally likely to lead the other in mutual ceremonies and both males and females sometimes Scraped separately.

PREPARATION OF THE NEST SCRAPES

One or 2 days before the laying of the first egg, nest-site searching ceased. The male returned to several of the depressions previously formed by Scrap-

ing (scrapes) and began to pull up dead grass and fresh grass if present. The position of the body while pulling grass strongly suggested Ground-Pecking and is likely the behavior from which that display is derived. After several hours at each scrape, circular areas about 10 cm in diameter were denuded except for the larger rootlets. Scrapes were considered complete when denuded to a diameter of 10 cm, this being the average diameter of nests. Sometimes the male divided his activity among several different sites before completing any. Typically 2 or 3 were completed and several were left incomplete. One male repeatedly visited 6 or 7, performing scraping behavior in all of them and removing grass in several. After 2 hours, 2 of the scrapes had been denuded to diameters of 5 cm. In this particular case all of the scrapes visited were within 7 m of one another. In 2 other instances, however, scrapes denuded by a single male were nearly 30 m apart.

Höhn (1967) felt that the female Wilson's Phalarope was primarily responsible for denuding scrapes, but I found no evidence of direct participation by females. My observations at 6 nests from nest scrape preparation through egg-laying indicated that only males prepared the scrapes, although the females performed occasional Ground-Pecking behavior during Scrape Ceremonies and sometimes visited their mates while they were preparing scrapes. In the Red Phalarope (*Phalaropus fulicarius*), apparently only the male prepares and builds the nest as well (H. Mayfield, pers. comm.). It is not known, however, if Red or Northern phalaropes denude the nest scrape before the first egg is laid.

TERRITORIAL BEHAVIOR

Male territorial behavior was observed only once during the nest scrape preparation period. On 27 May 1970 a lone male was active at several scrapes when a pair began nest-site searching in the same area. As they passed within 3 m of the male, he crouched low for several seconds, directed a "Flying Threat" (see Howe 1975, for threat descriptions) at the male of the pair, and then gave several Flying Threats and "Head Forward Threats" to the female. Over a period of 2 hours the first male gave several Flying Threats and overt attacks, most of which were directed at the female of the pair although she had directed no displays toward him. The female responded to the attacks with several "Bill-Downs" (BD, see below), a display probably serving an appeasement function. The pair remained in the area despite the frequent attacks, which continued even after the pair had moved 25 m away from the area where the first male was clearing nest scrapes. Finally the male flew in and hovered over the female of the pair and gave the "*Ernt*" call characteristic of aerial chases (see Howe 1975). The pair and a second female joined the male in a short aerial chase which ended in the nearest slough. This was clearly an attempt by a male to defend a small area

around the nest scrapes he was preparing. I observed no other case of direct competition for a nesting area.

After the onset of incubation, a male did not actively defend the nest area unless an unpaired female followed him back to the immediate vicinity of the nest. Since I found active nests as close as 5 m apart, any territorial tendency present during nest scrape preparation was apparently lost by the time incubation began. Nests of the Northern Phalarope have been found 1 pace (Selous 1915) and 5 paces (Höhn 1971) apart; 2 nests of the Red Phalarope were found 7 paces apart (Rüppell 1968). These observations suggest that males of all species of phalaropes do not exhibit strong territorial behavior, if any, during incubation. However, the males in question could have been mated to the same female.

Females were territorial in the sense that they defended the mobile positions of males during the courtship period, but only twice did I observe females exhibiting behavior which might have represented defense of a breeding area. In each case a swimming female threatened another with Flying Threats in the apparent absence of any males. I could not be absolutely certain that no males were present, however, and the possibility of feeding competition in these isolated instances could not be ruled out. Therefore I have not recorded any definite examples of females exhibiting territorial behavior related to a breeding area. This conclusion agrees with that of Höhn (1967) for Wilson's Phalarope. Tinbergen (1935) presented evidence suggestive of territorial behavior in breeding female Northern Phalaropes but Höhn (1971) was unable to corroborate these observations. Neither Höhn (1971) nor Bengtson (1968) felt that the Red Phalarope exhibits territorial behavior although the function of female "circle-flights" observed by the latter is not clear.

COPULATORY BEHAVIOR

Successful copulations probably occurred mainly in well-established pairs but unsuccessful attempts often took place in the early stages of pair formation. Either sex initiated a copulatory sequence, which sometimes included several highly ritualized precopulatory displays. Copulations took place while the birds were standing in shallow water or on shores of sloughs. Only 1 of 51 copulations or copulation attempts I observed took place between birds swimming in deep water. My observations conform to those of Höhn (1967) but differ strikingly from those of Johns (1969), who recorded 37 swimming copulations of a total of 53 observed over a 5-year period. According to Johns (pers. comm.), the bodies of water on his Montana and Washington study areas had an abundance of shoreline suitable for standing copulations, so it is difficult to explain why swimming copulations were so

frequent. Possibly Johns misinterpreted some overt attacks on females by males as copulation attempts, since he noted that "in these cases the male lit on the swimming female's back and pecked lightly at the top of her head for the 2 to 4 seconds of the act" (Johns 1969:665). I rarely observed head-pecking except during attacks and most copulations I observed lasted longer than 2 to 4 sec (see below).

Some of the pre-copulatory displays of Wilson's Phalarope have been described and illustrated by Höhn (1967). He concluded that behavior associated with copulation varies greatly but that a complete sequence includes the "Head-Up" and "Head-Down" postures. He observed one Head-Up posture (in a male), which he described as a rigid pose with the neck extended vertically and the bill pointed upwards at a 45° angle. In observations of 51 copulations I recorded this posture only once and it was performed by a female.

More frequent was the posture I call the "Pre-Copulatory Upright" (PCU, Fig. 1e). The PCU posture by the male preceded every mount I observed and was probably what Höhn (1967) described for one copulation as a "partially erect pose." In PCU the bird stood erect with the neck extended vertically but, unlike Höhn's Head-Up, the bill was directed forward. A male in the PCU posture made many rapid treading movements slightly forward, backward or sideways. The head remained more stationary than the rest of the body and consequently the neck and body appeared to sway back and forth. Orientation with respect to the female was variable. Sometimes the sequence ended at this point: otherwise the male moved around to the rear of the female and attempted to mount. PCU was usually performed simultaneously by both sexes but the female's neck was often partially dilated suggesting that the *Chug* call (see Howe 1975) was being given. In one case 2 birds faced each other in PCU pecking lightly at each other's bills before the male moved around to mount. PCU occurred almost simultaneously in both sexes but, in 6 cases observed under especially favorable conditions, the female initiated 5.

The PCU was often the only obvious pre-copulatory display. The forward and backward treading movements suggested expression of conflicting tendencies to approach and withdraw. The extended neck (resembling a pre-flight posture) and occasional running away (usually by the female) while maintaining the PCU posture suggested the predominance of a withdrawal tendency. The extended neck might be a prolonged and partially ritualized pre-flight posture. The PCU was typically held for 3 to 10 sec.

The Head-Down pre-copulatory posture, observed by Höhn (1967) in both sexes, sometimes occurred as a preliminary to PCU. However other postures with a lowered head were also used and the relationships between these pos-

tures are confusing. Because of the difficulty of distinguishing among them I have grouped them under the term "Pre-Copulatory Bow" (PCB). The form described by Höhn (1967) (PCB Type II, Fig. 1c) is apparently the rarest. More common is a posture similar to scraping (PCB Type I, Fig. 1b). Both are rigidly maintained but at least one intermediate between them occurs (PCB Type III, Fig. 1d). The PCB might better be interpreted as a continuum of display postures reflecting varying strengths of tendency to copulate. These displays last for only a few seconds, but once I observed a female maintain the posture for 15 sec. A similar-appearing display, the Bill-Down (BD), also occurred in pre-copulatory situations but probably has a different motivational basis and evolutionary origin (see below).

Many similarities exist between some pre-copulatory behavior and the behavior of pairs engaged in nest-site searching. PCB Type I is similar to a bird Scraping in a nest cup. PCB Type II closely resembles Ground-Pecking. Both forms were often given by females early in pair formation after attempting to lead a male away from the shore. The temporal overlap of copulatory and nest-site searching behavior during the breeding cycle led to situations in which tendencies toward each were present at the same time. It is not surprising, then, that pre-copulatory displays of Wilson's Phalarope appear to have been in part derived from behaviors directly related to nesting.

A female epigamic display, "Chugging," was frequently used during the courtship period (Howe 1975). In this display the neck is extended vertically, the throat dilated and a repetitive, low-pitched, frog-like call given. As pointed out above, the same call was possibly given during the PCU display. Chugging was also given by females at the beginning of about 25% of the copulatory sequences (usually incomplete) I observed. In an established pair Chugging did not elicit an aggressive reaction on the part of the male as it often did during social courtship. When members of a pair were not both sufficiently motivated for copulation, a series of Chugging, PCB's, PCU's and BD's (see below) might go on sporadically for several minutes without copulation being attempted. Chugging may have occurred more frequently in pre-copulatory situations than I have recorded, since the call is faint and difficult to hear.

No other pre-copulatory displays were observed. Particularly striking was the absence of wing-quivering with the wings held high over the back, a pre-copulatory display characteristic of many tringine sandpipers, the closest relatives of phalaropes (Jehl 1968). There were no post-copulatory displays. Behavior following copulation was variable but most often the pair flew away with the female in the lead. These flights are discussed in detail below (see "Pair Flights").

Seven complete copulations timed from the onset of pre-copulatory behavior

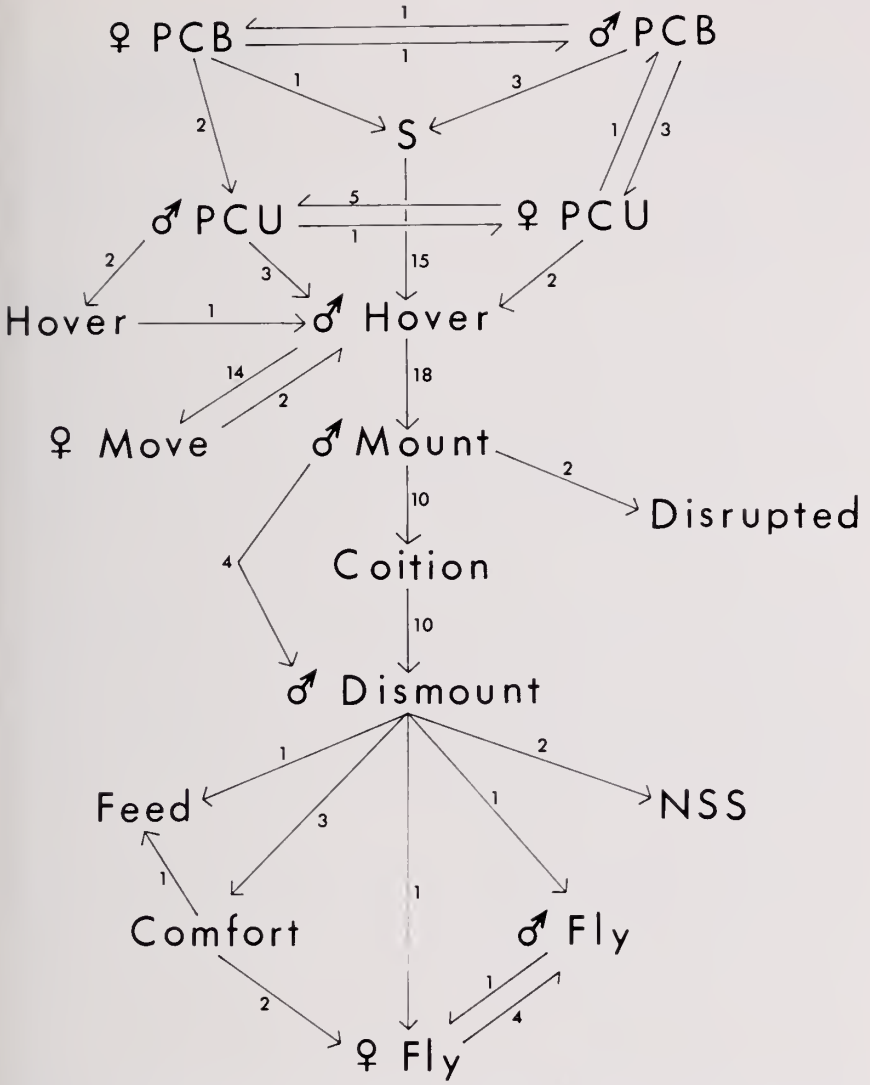

FIG. 2. Flow diagram of behavior sequences during 34 complete or incomplete copulations observed from the onset of pre-copulatory behavior. "Chugging" (see text) is not included. PCB = Pre-Copulatory Bow. PCU = Pre-Copulatory Upright. S = Virtually simultaneous PCU by both sexes. NSS = Nest-site searching.

(excluding Chugging) to the dismount averaged 46.5 sec with a range of 27 to 68 sec. A flow chart of copulatory behavior is presented in Fig. 2. The frequency of copulations is not known, although one pair copulated twice within 85 min.

OTHER BEHAVIOR PATTERNS OF PAIRING AND PAIRED BIRDS

Hostility existed between members of the forming pair, even during the early stages of nest-site searching. The male often showed intolerance of the female when she was closer than .5 m and mutual Scrape Ceremonies were occasionally interrupted momentarily by male threat. Hostility between the members of the pair gradually disappeared during the nest-site searching period. Several behavior patterns, in addition to Scraping, seemed to function in part as hostility-reducing mechanisms:

Preening.—A normal period of preening in unpaired, migrating Wilson's Phalaropes lasted about 8 to 10 min. but 2 pairing birds often spent up to 25 min preening as they stood only several cm apart. While preening the birds usually faced in the same direction but occasionally they would face one another without showing hostility. In other contexts facing at close range was rarely tolerated. Similar prolonged and possibly ritualized preening occurs in many avian species during and after pair formation and may facilitate adjustment of one sex to the close presence of the other. Allopreening was never observed.

Bill-down (BD) displays.—These displays were observed 29 times in females and 5 times in males. The form of the BD was variable; the 2 extremes are illustrated in Figure 3a and b. Of the 34 records, 16 occurred prior to precopulatory sequences, 5 during periods of nest-site selection and 13 when a male and female were simply in close proximity and facing each other. All were given while facing the mate at a distance of 1 m or less. BD's lasted only for a fraction of a second but sometimes were repeated 3 or 4 times in rapid succession.

Two observations suggest that BD's had an appeasement function. In each case the female of a pair flew in to join her mate, eliciting a Head Forward Threat from the latter. The female immediately responded with BD's and male aggression ceased. BD's presumably minimize the threatening potential of the bill. Since all observations of BD's involved birds close together in later stages of pair formation, it is likely that the display served to reduce aggressive tendencies in the mate, permitting the 2 birds to remain close to each other. The display appeared to be almost identical to precopulatory "Pushing" in Red Phalaropes (Bengtson 1968, Andrew 1955) except that in Pushing the female actually comes into contact with the male.

BD displays of the Type I variety (Fig. 3a) resembled normal breast preening but were easily distinguished in being very brief and regularly rhythmic when several were given in succession. It seems likely that these displays have been ritualized from preening behavior. On 5 occasions I observed birds perform apparent displacement preening of the breast during precopulatory

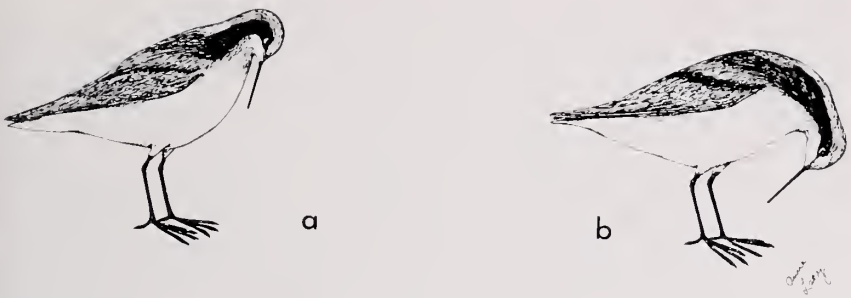

FIG. 3. Bill-Down Displays: a. Type I; b. Type II.

behavior or Scrape Ceremonies. Each case involved a male and female in close proximity, a situation in which BD's could be expected to occur. The form of BD Type II (Fig. 3b) was reminiscent of belly-preening but also resembled PCB Type II (Fig. 1c) and might be considered to be derived from a "typical compromise" (Morris 1957) of the latter and BD Type I.

Vocalizations.—Several calls, most given by both sexes, were used during the final stages of pair formation. All were of low amplitude and were effective only for short-range communication. The brief, nasal "contact *Ernt*" call (Howe 1975) was the commonest and probably served as a pair-bond reinforcing signal and/or as a mechanism for maintaining contact during visual isolation. Often contact *Ernts* were repeated antiphonally for several seconds by members of a pair. Some observations suggest that such duetting might function to reduce the distance between birds. In one pair I watched for 2 hours, antiphonal contact *Ernts* were given frequently when the birds strayed apart while feeding. Usually one bird responded by flying in, landing close to the mate and resuming feeding activity. Several other distinct calls were given during pair formation (Howe 1972) but were less frequently heard than contact *Ernts*. The functions and physical characteristics of these calls will be reported elsewhere in detail.

Pair flights.—Among well established pairs I commonly saw the female initiate pair flights in which the male followed closely at several m or less. These flights could be short, simply from one side of a slough to the other, or long, possibly to the nesting area. Pair flights often took place shortly after a successful copulation and were at least sometimes preceded by an exchange of antiphonal contact *Ernt* calls (Howe 1972). Unlike the erratic aerial chases of early courtship (in which the male leads), pair flights usually followed a straight path, although the birds might circle back immediately before landing.

There appeared to be certain ritualized elements in the flight pattern of

females in pair flights. In contrast to normal flight, the wing beats were more rapid, the neck was somewhat extended, and the forward progress was unusually slow. These features indicate a possible relationship to the "Ceremonial Flight" of Northern Phalaropes, a circular flight performed by females (Tinbergen 1935). The ceremonial flight could be a ritualized form of a pair flight in which the male does not follow. If a male Wilson's Phalarope did not take flight with the female, she circled back and landed near him.

The functions of pair flights are not obvious. They possibly function as tests of pair bond strength during the critical period immediately before laying. They may also be a means of luring the male back to the area of the nest scrapes and communicating laying readiness. There are probably functional analogues in other shorebirds, such as the "Joint Flight" of Black-tailed Godwits, which Lind (1961) believed to be derived from the sexual pursuit. Such a derivation is not possible, however, in the phalaropes because the sex roles in aerial chases (sexual pursuits) and pair flights are reversed.

THE EGG-LAYING PERIOD

While the male was denuding nest scrapes, the female spent much time concealed in dense sedge sloughs. Presumably, at this stage of the nesting cycle, the female required additional food for egg production and consequently spent more time feeding. If the nest scrapes happened to be near the slough where the female was feeding, contact *Ernts* were occasionally exchanged by the members of the pair. Periodically the female walked out of the slough, calling with contact *Ernts* and joined her mate in a Scrape Ceremony at the scrape where he was working. Following the ceremony, she either walked or flew back to the slough. If she flew the male usually followed and copulation often took place. These visits to the scrape may have indicated the female's readiness to copulate. I did not determine whether females visited their mates when the nest area was far from the feeding slough.

Shortly before the first egg was laid, the male spent much time at the scrapes. When he left, he joined his mate in the slough where she was feeding. Since the birds did not defend areas away from the immediate vicinity of the scrapes, there was frequent mingling with other conspecifics at the feeding, loafing, and copulating areas. By this time the aggressive roles of the sexes had changed. Whereas earlier in pair formation the female aggressively defended her potential mate and the male rarely threatened, now the male threatened other conspecifics, especially courting females, and his mate rarely showed hostility. The only times I observed females exhibiting threat behavior during this stage of the breeding cycle were when copulations were interrupted by a nearby female or male. Höhn (1967) also noticed an in-

crease in male aggressive behavior later in the season but did not relate it to this specific period of the breeding cycle.

I watched 5 pairs extensively during the egg-laying period. Since I never observed laying of the first egg, however, I do not know whether the female visited more than one scrape before laying as Tinbergen (1935) observed in the Northern Phalarope. At several nests I was able to observe behavioral interactions between the sexes at the nest during and between the layings of the second, third, and fourth eggs. At these times I often saw the female walk out of the sedges of a nearby slough, proceed part of the way toward the nest and then return to the slough. Contact *Ernts* were exchanged between her and the male at the nest. As much as 2 hours before actual egg-laying time the female went to the nest, usually by an indirect route. She adopted the Scraping posture at the edge of the nest, which was being attended by the male, and a Scrape Ceremony would follow. Whether or not the ceremony was performed, the male then Crouch-Walked away and the female replaced him on the nest. During these visits to the nest the female performed nest-building movements and egg-laying sometimes occurred. Meanwhile the male remained about 2 m from the nest, preening, or else he flew to a nearby slough. These encounters differed from similar encounters during the nest-scrape preparation period in the longer period of time the female remained on the nest, performance of nest-building movements by the female, and the male's departure from the nest site. The use of the Scrape Ceremony during nest relief has been described in the Black-tailed Godwit (Lind 1961), Redshank (*Tringa totanus*) (Grosskopf 1959), Northern Phalarope (Tinbergen 1935), and other species.

When both members of a pair had been away from the nest during the egg-laying period, the male might return alone or both might return together. In the latter case, either sex could lead as the birds approached the nest, but the male was usually first to enter the nest (Table 2). The female then either walked away or replaced the male in the nest following the usual Scraping posture or Scrape Ceremony. Often both birds uttered rapid contact *Ernts* or variants thereof as they approached their nest. Other vocalizations audible only at very close range were sometimes given.

If an egg was not laid during the female's visit to the nest, she walked or flew back to the slough. During each of 5 actual layings I observed, the male flew to a nearby slough after being relieved at the nest. Females remained on the nest for an average of 13.8 min (range 10.5–17 min) at each laying and then flew directly to a slough. Before flying from the nest, each bird opened its bill slightly as if vocalizing.

Intervals between 2 consecutive layings were determined accurately in 3 cases: 25.5, 26.0, and 27.75 hours. All eggs were laid on consecutive days

Table 2

Relative Positions of the Sexes Approaching and Entering the Nest During the Egg-laying Period

Sex Entering Nest	Position of Sexes Approaching		Totals
	Male Follow Female	Female Follow Male	
Male	4	6	10
Female	1	0	1
Totals	5	6	11

except once when at least 39 hours elapsed between layings. Höhn (1967) recorded 2 instances in which consecutive eggs were laid 2 days apart. The interval values I obtained compare with the following intervals for other shorebirds: Ruddy Turnstone (*Arenaria interpres*), 15–80 hours (Bergman 1946); Pectoral Sandpiper (*Calidris melanotos*), 24–29 hours (Parmelee, et al. 1967); Baird's Sandpiper (*C. bairdii*), 29–31 hours (Parmelee, et al. 1968); Sanderling (*C. alba*), 26–29 hours (Parmelee 1970); Dotterel (*Eudromias morinellus*), 39.9 hours (Pulliainen 1970).

The first egg of a clutch was deposited in a bare scrape. Shortly thereafter the male might begin lining the nest scrape with dead grass but the nest might also be ignored between the layings of the first and second eggs. Occurrence of the latter situation is based on periodic nest checks at which times the egg was cold and there was no evidence of lining. In gathering nest material the male faced away from the nest, tugged at dead matted grass stalks, and tossed them backward. This same behavior in the Black-tailed Godwit was termed "sideways throwing" by Lind (1961). It has also been widely reported among plovers and gulls. After tossing the grass backward, the male returned to the nest cup, avoiding the patches of thrown material. While sitting in the cup, he lined it by picking up and depositing the material in front of him or to one side. Several cup-shaping movements were performed and were apparently identical to those described by Lind (1961) for the Black-tailed Godwit. The lining was generally complete by the time the third egg was laid but building movements often continued into the first day or two of incubation.

Regular incubation behavior by the male generally began on the day the third egg was laid. On hot days, however, males would attend the eggs for several hours during earlier stages of the laying period.

Behavior of Females After Laying

After the fourth and final egg had been laid, the male returned to the nest to begin or continue incubation, and the behavioral mechanisms which

served to coordinate activities of the pair and maintain the bond ceased entirely. Observations were made on the subsequent behavior of 3 marked females. One remained in the immediate vicinity for 2 days and attempted to feed with her mate while he was off the nest between incubation bouts. Each time she approached within a few meters the male threatened her with a Head Forward Threat or Flying Threat. A second female also remained in her nest area for 2 days but did not associate with her former mate. Most of her activity was confined to a small portion of a large slough where she would utter sporadic contact *Ernts* at my approach and occasionally circle overhead, in the manner of a male flushed from a nest. Over the 2-day period she participated more and more in both short and long circling flights with other females. These flights were probably indicative of a developing flocking tendency since this bird completed laying on 4 June, the time at which post-breeding flocks of females began to accumulate on larger lakes.

I saw the third marked female in the company of a new male within several hours after completion of the clutch. Over a period of 5 min she gave 3 Head Forward Threats and 1 Flight Threat to another female. This was of particular interest since paired females rarely exhibited aggressive behavior. Although she soon became inattentive to the second male, the interaction suggested a return to behavior typical of the courtship phase. Tinbergen (1935) described a similar observation of Northern Phalaropes and suggested analogy with the performance of territorial behavior by certain bird species in the autumn. An alternative explanation, that at least some females attempt to pair successively with different males, seems more likely despite the opposing views of Höhn (1967) and Johns (1969). Recent studies (Raner 1972; Hilden and Vuolanto 1972) document the regular occurrence of serial polyandry in the Northern Phalarope.

Ovarian examinations of 10 females collected during the first week of June 1971 were made to determine the number of post-ovulatory follicles present. The results indicated that none of the females had laid more than one clutch, assuming that post-ovulatory follicles had not regressed beyond recognition. One bird, directing sexual displays toward a male when collected, showed possible signs of having laid eggs but the microscopic sections were inconclusive. These results, while not supporting the idea that Wilson's Phalaropes are polyandrous, do not rule out that possibility.

Female Wilson's Phalaropes were observed on the breeding grounds into the fourth week of June in North Dakota and some were still engaging in aerial chases, a feature of early pair formation, until close to the time of departure. Males off the nest between incubation bouts were often approached and followed in flight by females, which frequently adopted a hunched back posture with the neck retracted and head below the horizontal as in early

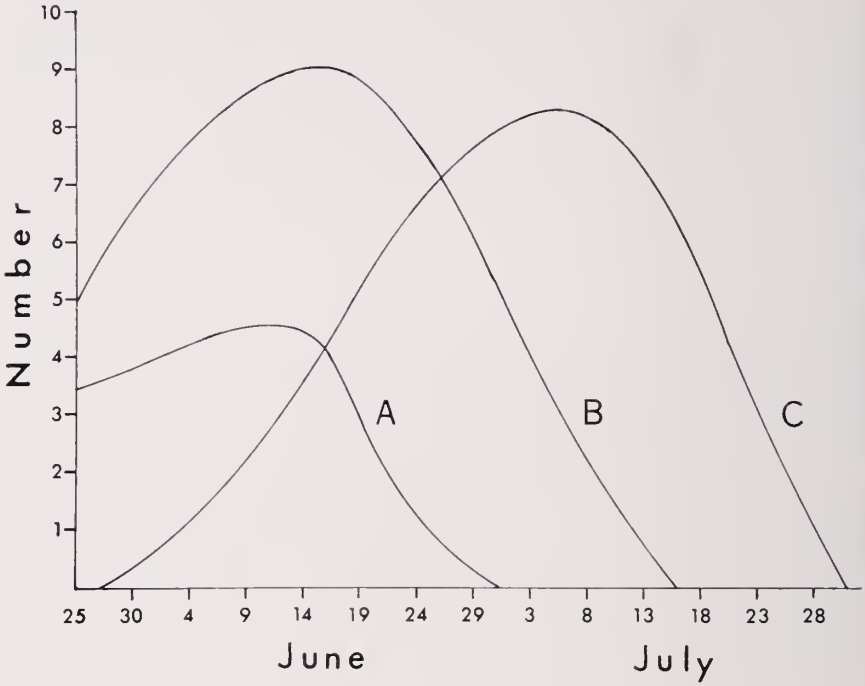

FIG. 4. Seasonal distribution of number of females observed on the main study area (A), number of clutches being incubated by males (B), and number of broods present (C). Data from 2 years were combined and averaged.

courtship (Howe 1975). Females even exhibited sexual interest in males attending broods and were especially attracted by males performing aerial distraction flights. I do not know whether any or all of these late females represented birds previously unsuccessful at obtaining mates. Their disappearance from the breeding grounds toward the latter part of June coincided with the time when most males were incubating and a few broods were already in evidence (Fig. 4).

DISCUSSION

Sex roles.—The pairing system of Wilson's Phalarope ranges from a period of intense competition for mates among females in social groupings to a period of pair isolation during which the behavior of males and females becomes geared toward attenuating intrapair hostility and coordinating sexual and nest-related activities. Although this general pattern of pair formation is shared by many species of birds, the reversal of sex roles in Wilson's

Phalaropes (and in other phalaropes) presents an additional facet with which the species must contend if successful breeding is to be achieved.

Female Wilson's Phalaropes, which are aggressive during early courtship, undergo a conspicuous reduction in aggressive tendency between the courtship and the egg-laying phases. During the same period the male acquires a complementary tendency to defend the pair bond against interference by conspecifics. Data presented in this paper indicate that the exchange of aggressive roles probably occurs about the time the potential nest sites have been selected and the male is preparing them for egg-laying. At this time the energy demand on the female for egg production may place severe constraints on her ability to continue active defense of the male. Hormonal changes accompanying egg production may inhibit aggressive expression as well. It therefore becomes adaptive for the male to take on the defending role, which includes defense of a small territory around the nest scrapes.

Female Wilson's Phalaropes are responsible for initiating nest-site searching and they participate as actively as the male during this process. They do not play a major role in nest-scrape preparation. In contrast, in most tringine sandpipers for which data are available, females play a less active role than males in nest-site searching and an equal or greater role in nest-scrape preparation. Males generally lead females in nest-site searching in the Black-tailed Godwit (Lind 1961), Redshank (Grosskopf 1959), Greenshank (*Tringa nebularia*) (Nethersole-Thompson 1951) and Willet (*Catoptrophorus semipalmatus*) (Vogt 1938). In the Greenshank (Nethersole-Thompson 1951) the female is apparently solely responsible for nest-scrape preparation. These tringines are apparently monogamous and the sexes share incubation. Sex roles in nest-site searching in the Northern Phalarope (Tinbergen 1935) follow the Wilson's Phalarope pattern of active female participation. Although the reason for the sex role differences in nest-site searching between Wilson's Phalaropes and tringines is not clear, it may be related to the fact that male phalaropes prepare the nests and therefore may require more precise cues from the female indicating readiness to lay.

Display homologies.—The displays used during the period of pair isolation by Wilson's Phalarope show much apparent homology with displays of other phalaropes but considerably less homology with displays of the more distantly related tringines. Chugging is probably homologous with the "Imposing posture" of Red and Northern phalaropes (Höhn 1971), in which the breast or neck feathers or both are fluffed and the head is held vertically. The Imposing posture has been observed as a female display during social courtship in both species and also as a female precopulatory display in the Northern Phalarope. No accompanying vocalizations have been reported.

Höhn points out the probable homologous relationships of the Head-Up

precopulatory display of the Red and Wilson's phalaropes, although the Head-Up is rarely given by Wilson's Phalarope from my experience (only 1 observation). The similar and more common PCU of Wilson's Phalarope has not been described for the other species. Interestingly, none of the phalaropes quivers the wings high above the back, a precopulatory display used by many tringines including the Redshank (Böcker 1958), Greenshank (Nethersole-Thompson 1951), Black-tailed Godwit (Lind 1961) and Willet (Vogt 1938).

No postures closely resembling the PCB's of Wilson's Phalarope (Fig. 1b, c, d) have been described for the other species. Höhn felt that Pushing in the Red Phalarope (Bengtson 1968), a display in which the bills are pointed down as a male and female make face-to-face contact prior to copulation, was homologous with the PCB. However, I consider the BD Type I (Fig. 3a) of Wilson's Phalarope the more likely homologue, and both are probably derived from displacement breast preening. No comparable display has been reported for the Northern Phalarope. The apparent absence of precopulatory displays with the head lowered in the Northern Phalarope may be a consequence of its preference for copulations in deep water. The only reference to a PCB-type display in tringines appears to be a Redshank display described by Böcker (1958), in which a rigid posture with head down and tail up is maintained for up to 1 min.

Displays related to egg-laying appear to be more highly developed in the Northern than in Wilson's phalarope. Tinbergen (1935) recorded a female Northern Phalarope performing several Ceremonial Flights before laying, with the male following her in each. The possible relationships between the Ceremonial Flight and the pair flights of Wilson's Phalarope were discussed above. After laying, the female and male Northern Phalaropes engaged in up to 20 Scrape Ceremonies, including Ground-Pecking (apparently identical to the display of Wilson's Phalarope, Fig. 1c), and the male also made several nest-building movements. This process was repeated at every laying by the pair he had under observation. By contrast, female Wilson's Phalaropes do not perform Ceremonial Flights, and after laying they fly directly from the nest to a nearby slough. The male does not remain at the nest while the egg is being laid. Possibly more mutual display is necessary to reinforce sexual recognition in the Northern Phalarope, which is less sexually dimorphic in plumage than Wilson's.

Polyandry.—The question of whether polyandry is a major force in Wilson's Phalarope breeding biology, or whether it exists at all, remains unresolved, although some investigators have considered Wilson's Phalaropes to be polyandrous. The history of these interpretations of observational data is reviewed by Höhn (1967), who concluded that no good evidence exists for

polyandry in the species. Johns (1969) agreed with this conclusion. Since that time Raner (1972) and Hilden and Vuolanto (1972) have found cases of serial polyandry in Northern Phalaropes. These were the first convincing published records of true polyandry in any scolopacid (*sensu* Jehl 1968). Raner (1972) also presented evidence of polyandry in the Spotted Redshank (*Tringa erythropus*). More recently a partially polyandrous system has been discovered in the Spotted Sandpiper (*Actitis macularia*) in 2 separate studies (Oring and Knudsen 1973, Hays 1973). Female Spotted Sandpipers occasionally incubate, however, suggesting a more flexible system than in Northern Phalaropes. Two other recently published studies describe highly flexible mating systems in 2 species of plovers (Charadriidae). Both the Mountain Plover (*Charadrius montanus*) and Dotterel show a range of systems including monogamy, polygyny, and polyandry (Graul 1974, and Nethersole-Thompson 1973). These studies make it clear that the possibility of serial polyandry in Wilson's Phalarope must be seriously considered despite the inconclusive evidence presented in this paper.

The ovarian examinations I made of breeding Wilson's Phalaropes did not show evidence of multiple clutches. However, the observation reported in this study of a female exhibiting sexual interest in a male shortly after laying a clutch for another male is suggestive of a tendency toward serial polyandry. An additional indirect line of evidence lends further support to this possibility. Lack (1968) pointed out that several species of scolopacid sandpipers lay unusually light eggs in proportion to body weight. Three of these species, Temminck's Stint (*Calidris temminckii*) (Hilden 1965), the Sanderling (Parmelee and Payne 1973), and the Northern Phalarope (Hilden and Vuolanto 1972), have been proven to lay multiple clutches. The latter authors point out that the Common Snipe also lays relatively small eggs and is known to produce frequent multiple clutches. Reducing clutch weight may be viewed as an adaptation for reducing energy demands on females which often lay more than one clutch (Parmelee and Payne 1973). Both Wilson's and Red Phalaropes lay proportionately small eggs, suggesting that multiple clutches may also occur in these species.

The mechanism by which a polyandrous mating system can evolve has long been unexplained. Recently, however, Nethersole-Thompson (1973) and Graul (1974) have independently advanced similar explanations for the evolution of polyandry in Dotterels and Mountain Plovers, respectively. The theoretical arguments have been especially well developed by Graul (1974). According to the latter, male Mountain Plovers in habitats experiencing severe fluctuations in food supply may be capable of raising a brood alone while the females, due to the energy depletion resulting from egg-laying, may be incapable of so doing. This situation commits the male

to increased parental responsibilities and leaves him vulnerable to desertion by the female. During favorable periods of food availability, the female may be able to recover enough energy reserves to lay a clutch for a second male. Graul discusses various ramifications of this idea.

This explanation may be applicable to phalaropes as well. Phalaropes occupy a unique feeding niche among shorebirds, often feeding on minute invertebrates taken while the birds are swimming in deep water. Although evidence is wanting, this feeding regime may experience fluctuations in food availability similar to those experienced by Mountain Plovers in arid grassland habitats. Detailed investigation of the phalarope feeding niche is certainly warranted and could provide the evidence necessary to explain polyandry in the Northern Phalarope, and possibly in other phalaropes.

SUMMARY

The behavior patterns of male and female Wilson's Phalaropes during the later stages of pair formation and the paired period are described. Females initiate nest-site searching behavior by leading males away from shores of sloughs into drier, grassy areas. During searching behavior each sex is equally likely to lead the other or both may wander in separate directions. Displays during this period are described and illustrated. The male alone prepares several nest scrapes for egg-laying by removing old and new grass, leaving a bare cup. A single observation of a male defending an area around the nest scrapes is the only evidence of territorial behavior by males observed in the entire study.

Pre-copulatory behavior is described and an attempt is made to quantify display sequences leading to copulation. There are no post-copulatory displays. The average duration of copulations is 46.5 sec. Only 1 of 51 observed copulations took place while swimming.

Paired birds and birds in the final stages of pair formation exhibit several behavior patterns which seem to function as aggression-reducing mechanisms. Most conspicuous are periods of ritualized preening and performance of Bill-Down displays. Flights in which the female leads the male are frequent at this time and may indicate laying readiness.

The female lays eggs in one of the prepared scrapes. The male is usually at the nest when she arrives and she replaces him. Usually the male flies to a slough where he is joined by the female after egg-laying, which lasts about 14 min. A clutch of 4 was usually completed in 4 days with an average interval between eggs of 26.4 hours. The male begins lining the nest with dead grass shortly after the first egg has been laid. Incubation is solely by the male and usually begins on a regular basis after the third egg is laid.

The male is hostile toward his mate soon after the last egg is laid and the bond is essentially dissolved at this time. There was one observation of a female directing sexual behavior toward another male after completing a clutch, but microscopic analysis of ovaries from collected birds did not show evidence of multiple clutches.

The motivational and evolutionary relationships among several displays are discussed and possible homologies with displays of other phalaropes investigated. The evidence for polyandry is examined in light of recent studies and one possible mechanism for its evolution is presented.

ACKNOWLEDGMENTS

This paper is based on part of a dissertation submitted in partial fulfillment of the requirements for the Ph.D. degree from the University of Minnesota. I am especially grateful to D. Frank McKinney for advice and guidance throughout the course of the study. Harvey K. Nelson and Leo Kirsch kindly provided housing, laboratory facilities, and logistical support at the Woodworth Station of the Northern Prairie Wildlife Research Center, U. S. Fish and Wildlife Service. Anne Lacy prepared the illustrations. Financial support was received through an NDEA predoctoral fellowship, grants from the Society of the Sigma Xi, the Frank M. Chapman Memorial Fund of the American Museum of Natural History, and NIH Training Grant 5 T01 GM01779 from the National Institute of General Medical Sciences. I would like to thank Joanna Burger and Walter Graul for reading and criticizing an earlier draft of this manuscript.

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NEST REPAIR IN LAUGHING GULLS

Celia L. Moore

The nests that Laughing Gulls (*Larus atricilla*) build in their marshy habitat along the coast of New Jersey are essentially 2-part constructions. First, a platform is built by carrying nest material, primarily dry *Spartina* grasses, to the site. As demonstrated by Bongiorno (1970), Laughing Gulls frequently select *Spartina* mats that have been formed by tide action as nesting sites. This gives the gull a more extensive platform capable of floating at high tide. Second, a simple concavity with a rim is formed by the Laughing Gull working from within the nest. In the normal course of nestbuilding, the Laughing Gull builds the rim gradually and more or less uniformly. It is possible for a well-constructed nest to be built of essentially random placement since the bird frequently changes its orientation in the nest, and alternates, in some undetermined fashion, between 3 different positions for placing the nest material: left, right, or directly in front. Alternatively, the gull may use information about the condition of the nest to determine the position in which it will place the nest material, the direction in which it will orient its body, or both. Both tactile and visual information from the nest rim are at least potentially available to a sitting gull.

Building while in the nest involves many different motor components, but the one that is of major importance here is the "sideways-building" movement described by Beer (1963a) for Black-headed Gulls (*Larus ridibundus*). It consists of reaching over the rim of the nest, picking up nest material in the bill, and placing it in the rim of the nest alongside the bird's body. The movement most frequently entails moving the head either to the left or the right before dropping the nest material, hence the name. Sometimes, however, the nest material is drawn directly toward the chest of the sitting bird and placed there. As in Black-headed Gulls (Beer 1963b), this behavior pattern is maintained throughout the incubation period of Laughing Gulls.

Moynihan (1953) has argued that nestbuilding during the incubation period of gulls is a displacement activity. It occurs inappropriately, he argues, when incubation has been frustrated in some way. It has been shown by Beer (1963b), however, that sideways-building is temporally related to rising and settling on the nest and independent of collecting nest material throughout the reproductive cycle. This suggests that the sideways-building components, but not the collecting components, of nestbuilding share causation with behavior patterns normally classified as incubation patterns. Thus, any manipulation that increases rising and settling will increase sideways-building.

My study was designed to determine if sideways-building could be altered, either in frequency or direction, by modifications of the nest during the incubation period. Specifically, the effects of (1) damaging and (2) wetting the nest on subsequent sideways-building activity were examined.

METHODS

Nests of Laughing Gulls on the Brigantine National Wildlife Refuge were marked and censused daily. The nests of 44 gulls in mid-incubation (1–3 egg clutches; median and mode = 2 egg clutch) were randomly divided into 3 groups and treated as follows:

Group D: Sixteen nests were damaged by having one-half the rim removed. Shears were used to cut through the rim so that a semi-circle of nest material could be removed. Alternate nests were cut on an east-west and on a north-south axis. The edges of the cut were marked with black waterproof ink.

Group W: Sixteen nests were marked in a manner corresponding to Group D, but the nests were not cut. Instead, a quantity of water (approximately a quart) was poured over half the nest, alternating sides as in Group D. This had the effect of saturating the nest material in half the rim, but did not leave water standing in the nest.

Group C: Twelve nests were marked as for the other 2 groups but were not further manipulated. For purposes of analysis, the half of the nest corresponding to the treated half of an experimental nest, matched on the basis of testing order, was scored as the "treated" half.

Immediately following the nest manipulations, 24 pieces of dry *Spartina* reeds, cut into 30 cm lengths and marked by dipping each end into black paint, were placed immediately alongside the rim of each nest. Half the pieces were placed on either side of the nest and were positioned so that their midpoint was at right angles to the cut, or the equivalent line drawn on uncut nests.

The nests were left undisturbed for 3 hours at which time they were revisited (3-hour check). Examination of the nests consisted of counting the number of marked pieces of nest material that had been incorporated into the nest and the number placed either wholly in the treated (damaged, wet, or matched control) or the untreated half. The nests were again left undisturbed until they were scored again the following day (24-hour check), to conclude the experiment.

The experiment was conducted on 3 separate and consecutive days with 20 nests treated the first day and 12 the following 2 days. The initial plan of having 20 nests in each group had to be abandoned when a storm and high tide decimated the remaining nests in the colony.

RESULTS AND DISCUSSION

Although all groups engaged in some nestbuilding activity during the first 24-hour period, neither manipulation affected rate of sideways-building as measured by incorporation of marked nest material into the nest (mean no. marked reeds in nest at 3-hour check: Group D—2.44, Group W—2.81, Group C—2.25; at 24-hour check: Group D—5.12, Group W—4.25, Group C—4.83). Thus, the presence of extra nest material within the reach of an incubating Laughing Gull stimulated some nestbuilding, but the likelihood of

TABLE 1

NUMBER OF MARKED REEDS BUILT WHOLLY INTO TREATED OR UNTREATED HALF OF RIM AT 3-HOUR AND 24-HOUR CHECKS.

Group	Treated	Untreated
	3-hour check	
D	21	1
W	6	8
C	4	2
	24-hour check	
D	31	5
W	7	11
C	4.5*	5.5*

* Half a broken reed in each half of nest. Unbroken reeds extending into both halves of the nest were not counted.

building under these circumstances was not increased by either a damaged or a wet nest.

Damaging the nest by removing a portion of the rim did, however, affect the pattern of sideways-building. Sideways-building was more frequently directed to the cut side of the rim as measured by comparing the number of marked reeds built into the treated half and the untreated half. Group D nests had significantly (Sign test $p \leqslant .03$: Siegel 1956) more reeds wholly in the treated half at both the 3- and 24-hour checks, while there were no significant differences in the way the 2 halves were treated by Groups W and C (Table 1).

Clearly, Laughing Gulls are capable of using information about the state of their nest to direct their sideways-building movements to areas of the rim where nest material is missing, even during mid-incubation. This contrasts to some extent with the behavior of weaver-birds. These birds will directly repair holes in their complex nests, but the repair behavior is best during the early stages of construction and may be aberrant or may not occur after the nest is occupied (Crook 1964). The control of nestbuilding behavior may change to some extent during the breeding cycle of Laughing Gulls as nests occupied by chicks are different from nests occupied by eggs. It would be instructive to investigate reaction to nest damage as a function of stage of cycle in this species.

Laughing Gulls did not respond to nest dampness as defined by this experiment by covering damp areas with additional nest material. If sideways-building is indeed adjusted to fit the wetness of the nest site, then Laughing Gulls may use more distal cues, such as level of high tide, for this purpose.

The results of this study lead to 2 conclusions. First, nestbuilding behavior of Laughing Gulls is directed by feedback from the state of the nest. Second, sideways-building can be modified by stimulation appropriate to nest-building even during the incubation phase of the cycle. These results add support to Beer's (1963b) contention that it is misleading to explain nestbuilding during incubation in terms of displacement.

SUMMARY

Nestbuilding activity of incubating Laughing Gulls was concentrated on experimentally damaged parts of the nest. This demonstrates that sideways-building is guided by feedback from the nest even when it occurs during incubation.

ACKNOWLEDGMENTS

I thank Drs. George F. Michel and Colin G. Beer for their assistance. I also thank the U. S. Fish and Wildlife Service for permission to work in the Brigantine Wildlife Refuge, and the Refuge Manager and his staff for their cooperation. The work was supported by PHS Grant #GM12774 to C. G. Beer. I was an NIH Predoctoral Fellow (No. 5 F1 MH-25,560) during the course of the experiment. This is publication No. 187 from the Institute of Animal Behavior.

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GENERAL NOTES

Opportunistic feeding of the Gila Woodpecker.—On 25 November 1973 we observed a female Gila Woodpecker (*Centurus uropygialis*) foraging in fremont cottonwood trees (*Populus fremontii*) along the Santa Cruz River at Kino Springs, northeast of Nogales, Santa Cruz Co., Arizona. Starting about 15:00 we observed the bird for approximately 15 min. The bird flew to the top branches of 12 m tall trees, and there picked leaves, one at a time, which it carried to the trunk of a nearby 10 m cottonwood tree and wedged into cracks in the bark with the petiole protruding. This activity was observed 5 times. In a sixth sequence the bird carried a leaf to a point about 7 m above ground and 10 m from the former deposit site. There it wedged the leaf into the crack of a broken off limb with the petiole again protruding. The bird picked, held, and manipulated each leaf with its bill, never using the feet. Each leaf was picked, held, and manipulated by its petiole.

The purpose of this leaf-picking was revealed by examining the first leaf placed on the tree. On its petiole and those of the other leaves picked by the bird was a gall, the brood chamber of the Homopteran, *Pemphigus populitranversus*. After the bird positioned the leaf on the tree it broke open the gall and removed insects. On one occasion we saw the bird pick a leaf, discard it, and pick another that it kept. The discarded leaf lacked a gall. A careful search in the small cottonwood grove revealed only 6 additional woodpecker-placed leaves, all having opened galls. These additional leaves were on the trunks of 2 trees adjacent the original tree. A search of the area on 3 February 1974 revealed only 1 more leaf wedged in the original tree trunk. By this late date all the leaves had fallen from the branches.

We collected 725 fallen leaves and found that 35.7% of these possessed galls. We assume this accurately reflected the percentage of afflicted leaves then on the tree. Thus, a woodpecker should have had little difficulty locating and picking a leaf with an afflicted petiole. Altogether 11 woodpecker-manipulated leaves were collected on 25 November, and the remaining contents of the galls were examined. Eight relatively fresh leaves with obviously unopened galls were selected from the ground leaf sample, and their gall contents also examined. The unopened galls held an average of 47.6 larvae and 46.5 imagines of *P. populitranversus*, whereas the opened galls held an average of 19.0 larvae and 2.3 imagines each. Thus, presumably an average of 28.6 (58.9%) larvae and 44.2 (95.1%) imagines were missing from each of the opened galls. This represents a maximum average number that might have been eaten by the woodpecker, as it is possible for imagines to escape. Nevertheless, this number appears to be representative for woodpecker predation. From the opened galls on the 5 fresh leaves that we observed picked by the bird only 25 imagines, an average of 5, were left by the woodpecker in each gall. In this case an average of 41.5 imagines were taken from each gall, and this is close to the 44.2 imagines thought removed from each gall. Also, the day of collection was cold and the imagines were not flying, nor were they crawling out of the galls until after the leaves and galls were placed in plastic bags and kept in our pockets. Furthermore, when we first opened the galls, we thought the larvae were dead. Of the 209 larvae 44% were still alive and in their open galls after 1 week in a plastic bag in a heated laboratory. We feel confident that our estimate of the numbers of imagines and larvae removed from the galls by the birds is fairly accurate.

While making the original observation on the Gila Woodpecker we also observed 2 Ladder-backed Woodpeckers (*Dendrocopos scalaris*; male and female) hanging up-side-

down from the upper-most small twigs hammering at the galls and seemingly obtaining food from them, all without removing the leaves. This process continued uninterrupted for the half hour we were in the area. A question arises as to the commonness of the behavior exhibited by the Gila Woodpecker. Inquiries to several colleagues yielded only one similar observation. On 17 April 1973 Russell P. Balda (pers. comm.) and several students on a field trip to Montezuma Castle National Monument, Yavapai Co., observed 2 Gila Woodpeckers picking gall-infected cottonwood leaves and placing them in the forks of the upper branches where the galls were opened and their contents eaten. Cottonwoods occur in only a small part of the Gila Woodpecker's range—in riparian areas in the desert and in adjacent higher areas. *P. populitranversus* was common in 2 of the 5 groves we inspected in Santa Cruz and Pima Cos. Thus the leaf-picking-stuffing-opening behavior is probably, at best, uncommon in the Gila Woodpecker.

The behavior we observed is similar to that employed by this species to use food resources as reported by Phillips et al. (The Birds of Arizona, Univ. Ariz. Press, Tucson, 1964). Apparently only the European Great Spotted Woodpecker (*Dendrocopos major*) is also known to gather, place, and open galls in the manner reported here (Pfutzeureiter, Vogelwelt 78:120–123, 1957; H. Winkler, pers. comm.).

We thank G. A. Clark, Jr. and H. Winkler for their comments on an earlier version of this note, and the latter for sharing his interest in woodpeckers.—Steven Speich and William J. Radke, *Dept. of Biological Sciences, Univ. of Ariona, Tucson 85721.* *Accepted 24 Oct. 1974.*

Bahama Duck exploiting feeding habits of yellowlegs.—At 17:00 on 11 April 1971, while investigating the birdlife of Prickly Pear Island, north of Virgin Gorda in the British Virgin Islands, I came upon several groups of shorebirds and one Bahama Duck (*Anas bahamensis*) in a partially dried up salt pond at the southeast corner of the Island. The shorebirds included about 50 Lesser Yellowlegs (*Tringa flavipes*), 1 or 2 Greater Yellowlegs (*Tringa melanoleuca*), and 30 dowitchers (*Limnodromus* sp.). The yellowlegs were searching for food in an erratic manner while making slashing lateral bill movements.

Anas bahamensis feeds primarily on algae (Wetmore, Birds of Porto Rico, U.S.D.A. Bull., Bull. 326:29, 1916). The normal feeding posture is to submerge the head while paddling forward. This particular bird, however, would also rapidly swing its head and neck from side to side in a more exaggerated style than the yellowlegs pausing only periodically to breathe. For several minutes the duck fed directly behind an actively foraging yellowlegs and every movement of the shorebird was simulated by the duck.

The following morning I revisited the pond and again noted the Bahama Duck feeding in this manner and at times doing so behind a yellowlegs. At one point the Bahama Duck lost track of the yellowlegs whereupon the duck withdrew its head from the water, relocated the shorebird and paddled off hurriedly to follow it again.

There are various instances of anatids being involved in feeding associations. Bailey and Batt (Auk 91:488–493, 1974) mention various works that discuss ducks exploiting the wasteful feeding habits of swans. Siegfried and Batt (Auk 89:667–668, 1972) discuss feeding associations of Wilson's Phalarope (*Steganopus tricolor*) and Shovelers (*Anas clypeata*) in which the phalaropes fed trailing Shovelers; a reverse of the interaction presented in this paper. Christman (Condor 59:343, 1957), Parks and Bressler (Auk

80:198–199, 1963) and Emlen and Ambrose (Auk 87:164–165, 1970) describe several species of herons and the Belted Kingfisher (*Megaceryle alcyon*) benefitting from the feeding of the Red-breasted Merganser (*Mergus serrator*) and Hooded Merganser (*Lophodytes cucullatus*). Ducks seldom appear to benefit from feeding associations with birds of other orders.

There is minimal data in the literature on the feeding habits of *A. bahamensis*. Wetmore (op. cit.) analyzed stomach contents of 10 Bahama Ducks (both sexes) collected in Puerto Rico and found only vegetable matter in the stomachs of adults (all but one of which were in breeding condition). Though these data are scanty, that 2 reproductively active Bahama Duck hens had not eaten animal matter is interesting since Krapu (Auk 91:278–290, 1974) found that breeding Pintail (*Anas acuta*) hens feed significantly on animal material during the reproductive period.

I don't know if the Bahama Duck on Prickly Pear Island was a breeding bird. I saw over 60 Bahama Ducks in the Virgin Islands from 11–16 April with no indication of breeding behavior. While April is a key month in the breeding cycle of *A. acuta*, the nesting of *A. bahamensis*, as shown by the literature (Wetmore 1916; Struthers, Auk 40:469–478, 1923; Danforth, J. Dept. Agric. Porto Rico 10:1–136, 1926) is highly erratic.

I have not noted this feeding technique among thousands of other Bahama Ducks that I have observed in Puerto Rico, the Virgin Islands and Surinam, even though some of these birds were reproductively active and many were in salt ponds similar to this one and were closely associated with yellowlegs, or other foraging shorebirds.—Herbert Raffaele. *Dept. of Natural Resources, Box 5887, Puerta de Tierra, Puerto Rico 00906.* *Accepted 23 July 1974.*

The age at first flight for young American Ospreys.—Only generalizations regarding the duration of the preflight (nestling) period of American Ospreys (*Pandion haliaetus*) are found in the ornithological literature. Bent (U.S. Natl. Mus. Bull. 167:361, 1937) stated, "The young remain in the nest about eight weeks. I have seen the young leave the nest as early as July 26, but most of them do not leave until the first week in August or later [in Massachusetts]." Palmer (Maine Birds, Bull. Mus. Comp. Zool. 102:153, 1949) states, "Fledging probably requires about 55 to 65 days [in Maine]." More recently, Reese (Auk 87:747–759, 1970) indicated that young first fly at 6 to 8 weeks of age (in Maryland). Brown and Amadon (Eagles, hawks and falcons of the world, McGraw-Hill, N.Y., 1968) summarized information concerning the European subspecies (*P. h. haliaetus*) with the following statement (p. 199), "From about 42 days onward they perform vigorous wing-flapping exercises. They make their first flights at from 51 to 59 days, usually about 52–53. . . ."

Osprey nesting activities were recorded during intensive investigations of waterfowl nesting in offshore duck blinds along the upper eastern shore of Chesapeake Bay in Maryland in 1956. We visited nests as many as 10 times during the season and the dates of hatching and first flight were determined for the young in 18 nests. The mean hatching date was 25 May and the mean date for the first flight was 18 July (Table 1). The time to first flight varied from 48 to 59 days (mean = 54 days). This period represents the time between the date the first egg hatched and a member of the brood made its first flight. All members of the brood did not make their first flight on the same day. The findings were nearly identical to those reported for European populations.

Table 1

Date of Hatching and First Flight for Ospreys in Chesapeake Bay

Nest No.	Hatching Date	Flying Date	Days[1]
1	May 17	July 12	56
2	May 18	July 5	48
3	May 18	July 15	58
4	May 20	July 10	51
5	May 20	July 12	53
6	May 23	July 17	55
7	May 24	July 14	51
8	May 25	July 17	53
9	May 25	July 17	53
10	May 26	July 20	55
11	May 27	July 17	51
12	May 27	July 17	51
13	May 27	July 24	58
14	May 29	July 21	53
15	May 29	July 24	56
16	May 30	July 25	56
17	May 31	July 23	53
18	June 1	July 30	59
Mean	May 25	July 18	54

[1] Standard deviation was ± 2.95 days; therefore, the 95% confidence interval was 48 to 60 days.

The distance of the first flight varied according to the distance to acceptable perches. Flights from the offshore duck blinds varied from a few meters to 1000 m, but the majority were 200–300 m. The young do return to their nest after the first flight albeit awkwardly at times.—Vernon D. Stotts, *Maryland Dept. of Natural Resources, Annapolis 21401, and* Charles J. Henny, *U.S. Fish and Wildlife Service, Migratory Bird and Habitat Research Laboratory, Laurel, MD 20811 (present address CJH: Denver Wildlife Research Center, Building 16, Federal Center, Denver, CO 80225).* *Accepted 3 Oct. 1974.*

Diving times and distances in the Pied-billed Grebe.—Although numerous authors have investigated diving times of grebes, relatively few have reported data on underwater lateral movement. Jenni (Auk 86:355–356, 1969) found that Least Grebes (*Podiceps dominicus*) generally surfaced 5–10 m from where they dived. A Red-necked Grebe (*Podiceps grisegena*) remained submerged for over a minute, and moved more than 60 m underwater (Cahn, Auk 29:437–444, 1912). LaBastille (Wildl. Monogr. 37:1–66, 1974) recently has reported that Atitlán Grebes (*Podilymbus gigas*) have moved up to 90 m while remaining submerged. This paper reports diving times and lateral movement, under differing ecological conditions, in the Pied-billed Grebe (*Podilymbus podiceps*).

Pied-billed Grebes were observed at El Dorado Park, Los Angeles Co., California

Table 1

Diving Times and Distances of Pied-billed Grebes
(154 forage dives, 52 escape dives)

Type of dive	CV	Minimum	Maximum	Mean ± SD
		Diving Time in Seconds		
Forage	40.5%	1	15	7.58 ± 3.07
Escape	28.6%	3	18	9.31 ± 2.66
		Diving Distance in Meters		
Forage	81.8%	0	12	3.69 ± 3.02
Escape	44.3%	2	20	10.00 ± 4.43

during May, June, and July 1973, and February and May 1974, and at the U.S. Naval Weapons Annex, Fallbrook, San Diego Co., California during February 1974. Pied-billed Grebes were present on small, man-made lakes at both localities during all visits. Air temperatures ranged between 15.5 and 27° C, and water depths ranged from 2–5 m, with most dives occurring in water 2–3 m deep. Dive and pause times were recorded to the nearest second. Lateral movement, the distance between diving and surfacing points, was estimated to the nearest meter using fixed shoreline features and buoys as reference points. All observations were between 08:00 and 10:00, or between 17:00 and 19:00.

Two types of dives, escape and forage, were recorded. All dives occurring within 5 min after the observers' arrival and dives occurring after the grebes became aware of the observers were considered escape dives. Dives by grebes not responding in any obvious way to the observers were considered forage dives. The dive/pause ratio was calculated only from the mean values of forage dives and pauses. Only series containing 3 or more dives were used.

Data on birds diving in close proximity to one another were not recorded because positive identification was impossible. When grebes were not observed to surface within 60 sec they probably surfaced in nearby vegetation and the observations were terminated.

Forage and escape diving times (Table 1) were significantly different ($P < .001$; $t = 3.69$). The distance of lateral movement for forage and escape dives (Table 1) also differed significantly ($P < .001$; $t = 11.49$). Pied-billed Grebes submerged longer and moved farther during escape dives than during forage dives. These data indicate that the presence of a predator or potential predator influences diving time and distance. The dive/pause ratio of forage dives was 2.3, similar to the 2.7 reported for the Horned Grebe (*Podiceps auritus*) by Dow (Auk 81:556–558, 1964).

Mean distances moved during forage and escape dives approximate Jenni's (1969) observation that Least Grebes usually surfaced 5–10 m from where they dived. He attributed that movement to the pursuit of free-swimming prey by Least Grebes. Movements during forage dives in my study probably resulted from the similar feeding activity of Pied-billed Grebes.

Diving times reported here are similar to diving times by 2 *P. podiceps*, which averaged 9.37 ± 1.82 (SD) and 12.70 ± 2.77 (SD) sec per dive (Heintzelman and Newberry, Wilson Bull. 76:291, 1964). LaBastille (1974) observed 5 types of dives by Atitlán Grebes which averaged between 4.8 and 34.9 sec and varied with the age and sex of the individual birds. Jenni (1969) reported the average dive time for Least Grebes as 12.48 ± 0.59 (SE) sec. A Horned Grebe averaged 33.4 ± 0.72 (SE) sec per dive (Dow 1964).

Heintzelman and Newberry (1964) reported mean diving times of 2 Horned Grebes as 19.24 ± 6.11 (SD) sec and 17.38 ± 3.80 (SD) sec, respectively.

It is probable that differing ecological factors (Heintzelman and Newberry 1964, Jenni 1969), as well as interspecific behavioral differences, and possibly interspecific physiological differences, contributed to the variation in the diving times of various species of grebes. Intraspecific differences in diving times and distances occur under varying ecological situations among Pied-billed Grebes. Coefficients of variation (Table 1) suggest that escape dives are much less variable in both time and distance than are forage dives. This situation might be expected if birds diving to escape a predator were diving closer to their maximum times and distances. Forage dives, being more random in time and distance, exhibit greater variability.

Kathleen M. Bleich and Hans Megens helped with the field work. Most of the observations were made while I was a Ranger at El Dorado Park. Rear Admiral J. W. William, Jr., Captains W. E. Betzer and F. R. Cassilly, and Commander J. R. DeView provided access to Navy property.—Vernon C. Bleich, *Dept. of Biology, Rio Hondo College, Whittier, CA 90608; Present address: California Dept. of Fish and Game, Chino Fish and Wildlife Base, Rt. 5, Bird Farm Rd., Chino 91710.* *Accepted 24 Oct. 1974.*

Status of the Gyrfalcon in Illinois.—The Gyrfalcon (*Falco rusticolus*) was considered a species of accidental occurrence in Illinois by Smith and Parmalee (Ill. St. Mus., Pop. Sci. Ser. 4:21, 1955). Their record was based on a single individual in white phase observed on 20 December 1953 and presumably the same bird again on 27 December 1953 at Arlington Heights, Cook Co. (Lukasik, Aud. Bull. 89:8, 1954). The only other published occurrence of this species in Illinois is an observation made on 28 December 1966 at Illinois Beach State Park, Lake Co. by R. Gustafson (Fawks, Aud. Bull. 140:6, 1966); no other details were submitted with the report. Russell (Aud. Bull. 144:13, 1967) concluded from the few records of this species, its confusing variability in plumage, and the possibility that observations could have been made on falconers' escaped birds that the Gyrfalcon should not be included on the hypothetical list of Illinois birds. Russell also mentioned that no specimens or photographs of this species were extant for Illinois.

On 3 November 1971, an immature Gyrfalcon was trapped by Ken Invergo (a licensed Illinois falconer), 9.7 km S Galena, Jo Daviess Co., Illinois (apparently this is the same bird reported by Kleen and Bush, Amer. Birds 26:71, 1972, and Buckley, Amer. Birds 26:569, 1972, although they listed the date of capture as 6 November 1971). Appearing in poor condition, the bird was kept under observation and died sometime later. Dr. William Halliwell, of the University of Missouri at Columbia, performed an autopsy on the bird and concluded that it died from arterial hepatitis. The specimen (Ill. Nat. Hist. Surv. No. FA-r-1) weighed 1679.6 g and contained little fat. Although no gonad measurements were included with the autopsy, the specimen is assumed to be a female according to the measurable sexual differences listed by Friedmann (U.S. Natl. Mus. Bull. 50:637, 1950). On the basis of the length of the fourth primary the specimen is assignable to the subspecies found widely in northern North America, *F. r. obsoletus*. The plumage represents the gray phase (dark variety) described by Friedmann (1950: 636) and there were no signs of molt. This constitutes the first specimen record for Illinois.

Prompted by the discovery of a specimen, we canvassed other licensed Illinois falconers and learned that the Gyrfalcon has been trapped in Illinois at least 3 other times (sex was judged on size by respective falconers): 4 October 1966, Spring Bluff Forest Preserve, Lake Co. by Ken Sterner (immature female in gray phase, weight 1524.1 g when trapped); 7 January 1973, 4.8 km SE Esmond, De Kalb Co. by Ron Kern (first-year haggard female in gray phase, weight 1959.5 g when trapped); and 12 October 1973, 3.2 km E Roscoe, Winnebago Co. by Jack Oar (immature male in gray phase, no weight taken). All trapped birds showed no signs of captivity and behaved in the manner typical of wild caught falcons. Photographs of the trapped birds have been deposited with the Section of Wildlife Research, Illinois Natural History Survey, Urbana. Additional sight records include one individual observed in February 1964 at Chatsworth, Livingston Co. by E. C. Fitch; one observed 8 October 1972 at Spring Bluff Forest Preserve, Lake Co., by E. C. Fitch and Ken Sterner; and one observed in December 1973, 3.2 km SW Polo, Ogle Co. by Roland Lindsay.

Although there were 3 Gyrfalcons recorded for Illinois in 1973, there is no indication that this was a major flight year for the entire Midwest. Gyrfalcons have never been reported from Cedar Grove Ornithological Station, Wisconsin (D. D. Berger, pers. comm.), and are sporadic in occurrence in Minnesota. Perhaps the preponderance of records in 1973 is a reflection of more intense trapping and observation during this particular time period.

In light of these Illinois records and its reported occurrence in Iowa (Musgrove, Iowa Bird Life 19:22–23, 1949), Missouri (Moore, Bluebird 16:1, 1949), northern Ohio (Mosely, Auk 60:598, 1943), and Wisconsin (Stoddard, Auk 40:325, 1923; Gromme, Auk 55:273–274, 1938; Black, Auk 58:254, 1941), the Gyrfalcon should perhaps be considered a rare transient and winter visitant in Illinois.

We are grateful to E. C. Fitch, Ken Invergo, Jack J. Oar, Roland Lindsay, and Ken Sterner for their valuable contributions of data and to Daniel D. Berger for his comments concerning Gyrfalcons in Wisconsin.—Brooks M. Burr, *Illinois Natural History Survey, Urbana 61801; and* David M. Current, *202 S Dodson Drive, Urbana, IL 61801.* *Accepted 24 Oct. 1974.*

An encounter between a Turkey and a bullsnake.—At 08:40 on 31 May 1974 while making one of our spring-summer Rio Grande wild Turkey (*Meleagris gallopavo intermedia*) brood surveys in Brooks Co., Texas, we saw 2 adult female Turkeys on the ground under a motte of trees at approximately 30 m. We stopped our vehicle to observe the birds with binoculars to determine if they were accompanied by poults. No poults were seen. The peculiar behavior of one hen cautioned us to observe in more detail. She periodically picked up a snake in her beak and shook it back and forth. The Turkeys were frightened off when we got out of the vehicle in an attempt to photograph the event. The snake, a female bullsnake (*Pituophis melanoleucus*), appeared dead, but its muscles were still quivering. The snake was 140 cm long and weighed 314.6 g.

We put the snake in our truck to take to the lab for necropsy. In approximately 20 min the snake began crawling around in the truck, and we killed it. A necropsy performed by Dr. J. L. Kiel at the Texas A&M University School of Veterinary Medicine indicated the snake probably would not have died from the damage inflicted by the

Turkey to that time, but the bird may have continued her attack if we had not interfered. The bird had apparently pecked the snake several times on the head as multiple superficial wounds were present, and the brille and cornea of the right eye and the brille of the left eye were perforated. The only other external wound was 65.5 cm posterior to the rostrum where the Turkey apparently pecked the snake as she picked it up and shook it.

The conditions under which this Turkey-snake encounter took place are unknown. However, this event occurred during the normal nesting season for Turkeys. That there were only 2 hens in the group suggests they were involved in nesting activities since females in this area rarely occur in such small aggregations except during successful breeding seasons.

Though rarely reported, Turkey-snake encounters are not unprecedented. Jennings (Texas Game and Fish, 14[8]:3, 1956) reported a Turkey hen severely beating a 1 m rattlesnake with her wing.—Samuel L. Beasom and Oliver H. Pattee, *Dept. of Wildlife and Fisheries Sciences, Texas A&M Univ., College Station 77843.* *Accepted 29 Oct. 1974.*

Hooded Merganser kills a meadow vole.—On 27 August 1974 at 12:30, I saw an immature (1½ years old) male Hooded Merganser (*Lophodytes cucullatus*) kill a young meadow vole (*Microtus pennsylvanicus*) and attempt to swallow it. The vole, a female, was 83 mm long (body and tail) and weighed 9.1 g. The merganser was in an outdoor pen (4.5 m × 9.0 m) at the Patuxent Wildlife Research Center, Laurel, Maryland. It was hatched from an egg collected in the wild and artificially incubated and maintained on a diet of duck breeder pellets and dry dog food. The merganser caught the vole in tall grass at the edge of a water tank and bit down on the head repeatedly. After the vole was dead, the bird made several unsuccessful attempts to ingest it. I found that the vole's skull was completely crushed. On 29 August, I found a second juvenile vole dead in the water tank. It was a male, 95 mm long and weighing 10.0 g. Its skull was crushed also. These observations suggest that Hooded Mergansers may on occasion capture and ingest small mammals.

The food of Hooded Mergansers consists mainly of crustaceans, small fish, frogs, insects, and some vegetable matter (Kortright, The ducks, geese, and swans of North America, American Wildlife Inst., Washington, D.C., 1942; Bent, U.S. Natl. Mus. Bull. 126, 1923; Vermeer et al., J. Wildl. Manage., 37:58–61, 1973). I have found no report of small mammals being taken as food by Hooded Mergansers, although Salyer and Lagler (J. Wildl. Manage., 4:186–219, 1940) report shrews (*Sorex*) being found in the stomachs of two American Mergansers (*Mergus merganser*).—Donald H. White, *Patuxent Wildlife Research Center, Laurel, MD 20811.* *Accepted 7 Nov. 1974.*

Food washing by grackles.—It is well known that Common Grackles (*Quiscalus quiscula*) will place hard bread and crackers in water to soften them before eating (Bent, U.S. Natl. Mus. Bull. 211, 1958), but variations of this kind of behavior do not seem to have been recorded. At my winter home in Ocala, Florida, for years I have watched this species "dunk" bread in water. The local Common Grackles will do this

whether the bread is hard and dry, fresh, or even presoaked in water. The presoaked bread often disintegrates when it is rewashed. When the bread is still firm enough after soaking, it may be held in one foot and fed upon at the edge of the water, it may be carried away, or some or all of it may be left in the water and returned to later. Some individuals hold the bread in their bill, dip it in and out of the water, then fly away with it. Others drop the bread into the water and wait a few seconds before retrieving it. The bread often sinks, and a bird may immerse its head over its eyes to reach it. I have also seen grackles pick up a piece of dry bread, fly away with it, and then return to dunk it. I have never seen Common Grackles drinking in my yard, but have repeatedly seen them tip their heads back to let the water from well soaked bread run down their throats. Most of the bread dunking is done in a ground-level bird bath, but the birds will also use rain puddles on yard furniture and on the house roof.

I often run an insect trap in my yard at night, and habitually empty the specimens I do not need onto the ground the next morning. On 21 April 1973 I left a pile of insects, predominantly beetles but including a large mole cricket, near the bird bath. As I walked away a Common Grackle flew to the bath with a large mulberry in its bill. It perched on the rim and vigorously swished the ripe berry through the water. After it washed the fruit the grackle turned as if to fly, then noticed the insects on the ground. The bird immediately dropped the mulberry and jumped down to pick up the cricket. The grackle then returned to the bath, washed the cricket thoroughly, and after working it through its bill, flew away with the insect.

During the following year I found that this population of Common Grackles washes many kinds of food in water: both soft items, such as presoaked bread, and hard ones, such as local fruit and peanuts. When I put out whole raw peanuts, the grackles usually remove the nuts from the shell and then wash them. The peanut skin often comes off in the washing process.

An especially interesting incident occurred on 4 July 1974. A neighbor set out a half watermelon that had been only partially scooped out, and several of the local mammals, birds, and insects came to feed on it. The Common Grackles pried out pieces of fruit and washed them in the melon juice that had accumulated in a deep puddle in the rind.

I have looked for washing behavior in the Common Grackles at my summer home in Gaines, Pennsylvania, but have never seen it. When given hard bread the Pennsylvania grackles work vigorously at it, with one foot holding the food down, and they sometimes almost pull themselves over backward in their efforts. Although water is readily available at this location, apparently the soaking technique has never been learned by this population.

Similarly, all but one of the other species in my Florida yard have not learned the dunking technique. The single other instance of food washing I have recorded occurred on 10 February 1974, and involved a male Boat-tailed Grackle (*Cassidix major*). After watching Common Grackles dunking, it picked up a piece of bread and followed a Common Grackle to the water where the Boat-tail dunked before eating. Bent (op. cit.) notes bread soaking behavior in populations in Maine and Washington, D.C. My observations in Florida and Pennsylvania indicate that this behavior is widespread but not ubiquitous in Common Grackles. Clearly washing is not necessarily limited to particular types of food, hard or soft, natural or artificial. Apparently it is one of those types of behavior that, once learned by a local population, is performed relatively indiscriminately.

My thanks to Mary Clench for her help in writing this note.—Mary W. Wible, *517 NE 9th St., Ocala, FL 32670.* *Accepted 29 Oct. 1974.*

Another instance of incubation by a male Whip-poor-will.—There has been a difference of opinion as to the role of the male Whip-poor-will (*Caprimulgus vociferus*) in incubation. Raynor (Bird-Banding 12:98–103, 1941) reported that the male sat on eggs for brief periods, but Arnold (Michigan Biological Station unpublished MS, 1937, cited in Kendeigh, Ill. Biol. Monogr. 22:1–358, 1952) believed only the female incubated.

My observations at a Whip-poor-will nest in an oak forest in Allegan Co., Michigan (on the "Small Oak Area" of Brewer et al., Mich. Bot. 12:217–234, 1973) agree with those of Raynor that the male sits on the nest. I found the nest with two eggs on 30 May 1970 after flushing a female from the nest site on leaf litter in a clone of flowering dogwood (*Cornus florida*).

On my return visits in the next few days, the female would flush while I was still about 5 m from the nest and fly to a branch 8–15 m away. On 4 June, about 11:30, I set up a blind 10 m from the nest; I moved it to about 7 m from the nest 40 min later. The female did not flush when I entered or left the blind at this distance.

At 19:30, 4 June, the female was on the nest when I entered the blind. At 20:30, a male, identifiable by the white marking on the tail, alighted about 0.3 m from the nest. The female flew and the male walked to the nest, ruffled his feathers and settled over the eggs. At 20:37, the male flew from the nest, leaving the eggs uncovered. At 21:00 shortly after I heard two *whip-poor-will* calls nearby, a bird (sex unknown) was back on the nest. A bird was also on the nest when I checked, using a flashlight to produce eyeshine, at 03:35 and again at 04:00 on 5 June. At 05:00 and thereafter until I left the blind at 07:00, I could see the female on the nest.

I acknowledge the advice and editorial assistance of R. Brewer and comments on the manuscript by M. J. Mengel.—Ralph E. Babcock, *Dept. of Biology, Western Michigan Univ., Kalamazoo 49008.* *Accepted 12 Aug. 1974.*

Observations on the Aerial Drinking Performance of a Poorwill.—At 09:00 on 27 May 1973, I observed a Poorwill (*Phalaenoptilus nuttallii*) drinking water near my boat while the bird flew along the surface of the water. The location was a quiet cove on Amistad Lake north of Del Rio, Val Verde Co., Texas. The distance of the boat from shore was approximately 13 m when I noticed the bird. My attention was drawn to the fact that the Poorwill was only a few centimeters above the water's surface and did not appear to be feeding on insects. When within approximately 3 m of my boat the bird seemed to flutter its wings into a very tight vee over its back, lower its head with the mouth open and touch the water lightly, taking a drink. The bird repeated his performance several times then disappeared into the shadows. This type of behavior has been recorded previously for Common and Lesser Nighthawks (*Chordeiles minor* and *C. acutipennis*) (Bent. U.S. Natl. Mus. Bull. 176, Parts I and II, 1940) but to my knowledge, not for the Poorwill.—O. T. Fears, III, *Casa de Oro, Apt. 203, Weslaco, TX 78596.* *Accepted 19 Nov. 1974.*

On the death of a midwestern heronry.—What was the largest heronry in Illinois in 1962 (Bellrose, pers. comm.) no longer exists. Though I am unable to date the origin of this heronry, it existed since at least 1935 (Borgelt, pers. comm.). The end came suddenly, though not unexpectedly in 1973–74. Located east of the Illinois River,

2 km north of Pekin, Tazewell Co., Illinois, it contained 820 occupied nests in 557 trees in 1962 (Table 1). This heronry was situated on a natural levee resulting from a former meander of the Illinois River, and was one of three in the Illinois River Valley that I have observed yearly since 1962, (Bjorklund et al., Trans. Ill. State Acad. Sci. 60:107–108, 1967; Hammerslough and Bjorklund, Jack-Pine Warbler 46:57–61, 1968; Bjorklund and Canterbury, Proc. Peoria Acad. Sci. 4:27–28, 1971; Bjorklund et al., Ill. State Acad. Sci. News Letter 2(6):10, 1973). Great Blue Herons (*Ardea herodius*), Great Egrets (*Casmerodius albus*), and Black-crowned Night Herons (*Nycticorax nycticorax*) nested in the colony. Trees with nests were marked with numbered sheet metal tags throughout the period of the study.

The wooded levee on which the heronry was situated is bounded on the west by the old meander of the River and on the east by a flood-plain lake. Approximately 800 m south of the heronry the levee is permanently flooded, and only the stumps of dead trees emerge. The western bank is elevated slightly, sloping gradually (less than 1.0 m relief from the west edge of the levee) eastward to the lake. In the area of the heronry the levee is approximately 140 m wide (at mean water level). The principal species of trees and their former avian occupants are: cottonwoods (*Populus deltoides*), averaging 25 m in height, preferred by the Great Blue Herons; silver maples (*Acer saccharinum*), mostly 18–22 m, occupied principally by the Great Egrets; green ashes (*Fraxinus pennsylvanica*), mostly 14–17 m, occupied principally by the Black-crowned Night Herons. Many crowded and stunted black willows (*Salix nigra*), rarely used as nesting sites in this colony, and a few scattered slippery elms (*Ulmus fulva*) are also present. The cottonwoods grow along the western side of the levee lining the shore of the old meander. Silver maples grow in the central portion, while further east green ashes predominate. Black willows line the eastern edge of the levee. Frequent flooding prevents development of a continuous understory, poison ivy (*Rhus radicans*) and maple seedlings, along with small willows on the eastern side, being the only vegetation of significance other than the canopy trees.

Most of the site, including the heronry proper, was owned by the Pekin Rod and Gun Club until 1965. In 1965 the Forest Park Foundation purchased the land. It has since been sold to the State of Illinois for use as a managed conservation area.

I have witnessed repeated insults to the stability of the area. The disturbance having the greatest impact during the period of my observations began during the autumn and winter of 1962, when clear cutting of timber began at the north margin of the heronry and continued, illegally, after the Forest Park purchase (Table 1). Nests were abandoned in the area adjacent to the logged margin. It was my subjective impression that both egg and nestling mortality increased in the exposed locations. The colony retreated southward in the heronry, but the southern portion of the heronry could not be extended to offset the losses at the north end of the heronry. The portion of the levee south of the original heronry consists of smaller stunted trees located on ground subjected to more protracted flooding. Less than one kilometer south of the heronry many of the trees are dead or dying as a result of permanent flooding. The Central Illinois Light Company obtained a high line corridor through the area in 1958, altering integrity of the heronry and effecting a hazard for low flying birds using a nearby feeding ground. Additional high line towers were planned with construction scheduled to begin in 1974, though CILCO did agree to delay construction until after incubation and hatching would normally have been well underway. Partial draining of a flood plain lake located near a major steel and wire company, and pollution of unknown dimensions from various sources reduced the number of feeding habitats. Several nearby forested areas were con-

Table 1
Nesting Pairs of Herons
1962–74

Year	Occupied Nests	Great Blue Heron	Great Egret	Black-crowned Night Heron	Trees with Nests	Ave. Nests per Tree
1962	820	279	341	200[1]	557	1.5
Logging Began						
1963	751	124	272	355	373	2.0
1964	406	61	157	188	173	2.3
1965	475	50	192	233	187	2.5
1966	394	39	153	202	196	2.0
Logging Terminated						
1967	332	33	128	171	167	2.0
1968	83	28	49	6	35	2.4
1969	171	31	56	84	76	2.2
1970	235	29	70	136	106	2.2
1971	73	29	32	12	33	2.2
1972	216	41	58	117	92	2.3
1973	9	7	2	none	7	1.3
1974	none	none	none	none	none[2]	

[1] Estimated.
[2] Two remained from 1973 remnant nesting population.

verted to corn production. Wanton killing by man occurred from time to time, particularly after logging was initiated, when access to the area on foot at low water became increasingly easy. Also, I observed increased contacts between herons and owls as owls forced from their nearby nesting sites by the logging moved into the heronry and used heron nests (Bjorklund et al. 1967).

With the increase in human population, industry, highways, farming areas, and water and air pollution, it appeared unlikely that an abundance of any kind of wildlife could be maintained. Moreover the Illinois Department of Conservation, which now controls the area, was petitioned to raise the water level in an adjacent lake as a means for improving fishing. They denied the request to retain as much stability as possible in the area.

The prognosis for the long-term survival of this heronry was, from the beginning of my observations, unfavorable. Table 1 displays the population trend through 13 nesting seasons. While logging appears to have initiated instability, and many other factors appeared to contribute to the decline, the total collapse observed in 1973 was coincident with high water which inundated the heronry floor from late winter until mid-July 1973. This experience was repeated in 1974 when no nesting occurred (Table 1). I suggest that protracted high water was a factor contributing to abandonment. In 1974 I saw no Great Egrets or Great Blue Herons, and on only one occasion, 13 April 1974, did I see Black-crowned Night Herons in the heronry. On that date, which approximated the usual arrival time of this species (10-year average), 15 Black-crowneds were sitting in trees on the east edge of the heronry; I found no active nests. While many nesting pop-

ulations of herons in the Illinois–Iowa region declined in 1973, (Graber, pers. comm.; Bjorklund, pers. observ.; Kleen, Amer. Birds 27:874–875, 1973), only one other documented case of a similar complete collapse is known to me. Richard Graber has informed me that the "Heron Pond" colony SSW of Vienna, Johnson Co., Illinois, which had been in existence at least 20 years, contained about 60 Great Blue Heron nests and 12 Great Egret nests last spring. The Egret nests and possibly some of the Great Blue Heron nests were deserted before the end of the 1973 nesting season, and the birds did not establish nests in the 1974 season. The Heron Pond colony was in a cypress swamp having minimal human disturbance. Cause of that desertion is unknown.—Richard G. Bjorklund, *Dept. of Biology, Bradley Univ., Peoria, IL 61625. Accepted 24 Oct. 1974.*

Canada Goose parasitizing Mallard nest.—On 20 April 1974 in northwestern Cook Co., Illinois near Barrington Hills, an active Mallard (*Anas platyrhynchos*) nest containing 11 Mallard eggs and one Canada Goose (*Branta canadensis*) egg was found on top of a muskrat (*Ondatra zibethicus*) house. The muskrat house was wedged between two willows (*Salix* sp.) in approximately 60–80 cm of water at the wooded end of a .75 ha pond. Cattails (*Typha* spp.), sedges (*Carex* spp.), and creeping bent grass (*Agrostis palustris*) formed the predominate emergent vegetation. Willows and eastern cottonwood (*Populus deltoides*) were the dominant trees. The nest was checked each time we were in the area, a total of 10 times. On 17 May, following a 7-day period when the nest was not checked, we discovered that the nesting attempt had been terminated. We found no trace of the Mallard eggs; however three-fourths of the goose eggshell was present. The shell lining was present and intact on the shell. Rearden (J. Wildl. Manage. 15:386–395, 1951) gives a similar description for eggs eaten by raccoons (*Procyon lotor*).

On subsequent trips to the area, we watched for sign of a brood. On 30 May the carcass of a half-eaten Mallard duckling was found floating near the nest. The duckling was approximately 2 weeks old (Southwick, J. Wildl. Manage. 17:1–8, 1954). Two days later, with the aid of an Irish setter, I flushed a broody Mallard hen. Because no other nesting Mallards were found in the area, we assumed that this was the hen that we observed on the nest. Apparently the Mallard eggs had hatched successfully.

By using the age of the dead duckling, we estimate the date of hatching to be between 12 and 16 May. Backdating and using a 28-day Mallard incubation period, the egg-laying period was estimated to be approximately 14 to 19 April. During this period Canada Geese were known to have been in the area at least twice and there are several local flocks in the Cook Co. area.

Fannin (Auk 11:332, 1894) cites an instance of a Canada Goose laying eggs in the nest of an Osprey (*Pandion haliaetus*). Bent (U.S. Natl. Mus. Bull. 130, 1925) also reported an observation involving the same two species. Weller (Ecol. Monogr. 29:333–365, 1959) records the case of one Canada Goose parasitizing the nest of another.—Roger L. Boyer, *Landplan Systems, Commonwealth Associates Inc., 209 E. Washington Ave., Jackson, MI 49201, and* Mark J. Psujek, *Environmental Services, Dames and Moore, 1550 Northwest Highway, Park Ridge, IL 60068. Accepted 11 Nov. 1974.*

Carrion feeding by birds in southwestern Louisiana. From 15 May 1973 to 6 August 1974, along State Highway 27 within Sabine National Wildlife Refuge and

Table 1

Incidence of Carrion Feeding by Three Species of Marsh Birds, 1973–74

Carrion species	Boat-tailed Grackle		Red-winged Blackbird		Common Gallinule
	male	female	male	female	
Dragonfly (*Erythemis simplicicollis*)	—	—	10	—	—
Dragonfly (*Cannacria grauida*)	—	—	20	4	—
Alligator (*Alligator mississipiensis*)	4	—	—	—	—
Mud turtle (*Kinosternon subrubrum*)	3	—	—	—	—
Green water snake (*Natrix cyclopion*)	22	1	2	—	3
Broad-banded water snake (*Natrix fasciata*)	2	—	1	—	1
Cottonmouth (*Agkistrodon piscivorus*)	4	—	—	—	—
Least Bittern (*Ixyobrychus exilis*)	7	—	—	—	—
Common Gallinule (*Gallinula chloropus*)	4	—	—	—	—
Barn Swallow (*Hirundo rustica*)	1	—	—	—	—
Red-winged Blackbird (*Agelaius phoeniceus*)	2	—	—	—	—
Boat-tailed Grackle (*Cassidix major*)	2	—	—	—	—
Muskrat (*Ondatra zibethica*)	2	—	—	—	—
Nutria (*Myocastor coypus*)	10	—	—	—	—
Armadillo (*Dasypus novemcinctus*)	1	—	—	—	—
Total Observations:	64	1	34	4	4

along State Highway 82 between Johnson's Bayou and Holly Beach, Cameron Parish, Louisiana, we saw Common Gallinules (*Gallinula chloropus*), Red-winged Blackbirds (*Agelaius phoeniceus*), and Boat-tailed Grackles (*Cassidix major*) feeding on animals killed by motor vehicles. This behavior has been noted of several avian species (e.g. Long. Wilson Bull. 73:210, 1961; Hubbard and Hubbard. Wilson Bull. 81:107–108, 1969).

Of the birds we observed, Boat-tailed Grackles consumed more carrion than did the other two species (Table 1). Common Gallinules were rare carrion feeders. Bent (U.S. Natl. Mus. Bull. 211, 1958) reported that carrion consumed by Boat-tailed Grackles included ducks killed by hunters as well as mammals caught by trappers.

We rarely saw female grackles or female Red-winged Blackbirds feeding on carrion (Table 1). Possibly, roadside carrion may not be suitable food for nestlings, or females concentrate their feeding activities away from roads. All carrion feeders fed most often on the entrails of fresh roadkills though portions of decomposed animals were occasionally eaten by Boat-tailed Grackles.

Carrion have provided an easily acquired, abundant food source, but the adaptation to feeding on such materials sometimes has indirectly caused the death of the carrion feeder when it remained in the path of an oncoming vehicle.—Harland D. Guillory *and* Dwight J. LeBlanc, *Dept. of Biology, Univ. of Southwestern Louisiana, Lafayette 70501.* *Accepted 27 Nov. 1974.*

THE PRESIDENT'S PAGE

In my first "President's Page" (September 1973) I discussed the roles of some American ornithological journals, with special reference to The Wilson Bulletin. At that time I wrote: "In W.O.S. Council discussions in recent years, the prevailing opinion has been that The Wilson Bulletin should emphasize the publication of *field-based* studies. This leaves plenty of scope for variety, but reduces the amount of space available for (although we continue to publish papers on) anatomy, experimental (i.e., lab-based) physiology, some kinds of systematics, synthetic and theoretical ecology based on other people's field work, etc." In thinking about a subject for my last "President's Page," I became curious as to how closely The Wilson Bulletin has adhered to the balance of subject matter suggested above. I therefore made a rough (and admittedly somewhat subjective) analysis of the articles and general notes in the 1973 and 1974 volumes.

I divided "field-based" studies into 2 categories. In the first, in which most of the gathering of the *data* was done in the field, there were 120 papers (66%). In the second category were studies in which the authors themselves collected their *materials* in the field for later indoor analysis. These materials included bird specimens, egg shells, pellets and droppings, nests, parasites, and sound recordings. There were 33 such papers (18%). Non-field studies were also divided into two categories. Laboratory studies of living birds accounted for 13 papers (7%) and indoor studies of all other kinds for 17 (9%). With 153 field (84%) and 30 non-field (16%) studies published in these years, it seems that our suggested emphasis is being practiced.

The question naturally arises as to whether these figures simply reflect the thrust of current ornithological research in general. To test this possibility, I assumed that The Auk probably publishes an accurate cross-section of ornithological research, and applied the same 4 categories to the papers published there during the same 2 years. I found that 56% were primary field studies, 18% were studies of materials collected in the field by the authors, 11% were studies of captive birds, and 15% other "indoor" studies. The division for The Auk was therefore 74% field-based and 26% non-field-based papers, versus 84% and 16% respectively for The Wilson Bulletin.

Refining the classification, the Wilson Bulletin papers fell (or could be forced) into 18 subject matter categories. The largest of these was behavior, including vocalizations (40 papers). Then came various aspects of reproductive biology (35), followed by food, water, and foraging, with 26 papers. Distributional information was the topic of 23 papers. Broad-scope studies of the biology of single species (in one case a comparative study of 2) accounted for 13 papers. I "lumped" parasitology, pathology, pesticides, and trauma, which collectively included 10 papers. The remaining categories, in roughly descending sequence, were taxonomy, plumage and molt, populations, fossils, physiology, migration, anatomy, predation on birds by nonavian predators, hybridization, techniques, eggshells, and a specimen census.

I made a geographic breakdown of the field-based studies and found, as expected, that most were done in the continental U.S. (114) or Canada (13). Other areas included Mexico (4), Bahamas (3), Colombia, Costa Rica, Hawaii, Jamaica, Peru, and Trinidad (2 each), and Antarctica, Australia, Ecuador, England, Guyana, Ivory Coast, Madagascar, Okinawa, Paraguay, Puerto Rico, Surinam, Tonga, and Venezuela (1 each). One author didn't mention where the field work was done!

Omitting faunal and other multispecies studies, the subjects of the Wilson Bulletin papers belonged to 46 avian families. The ten most popular groups for study were the Icteridae (16 papers), Anatidae, Laridae (10 each), Parulidae (9), Accipitridae, combined Strigidae-Tytonidae (8 each), Emberizidae (7), and Picidae, Turdinae, and Carduelinae (6 each).

I think this diversity of subject and approach is encouraging, and a good indication that The Wilson Bulletin contains "something for everyone." KENNETH C. PARKES.

ORNITHOLOGICAL NEWS

From its inception until 1971, the Biological Society of Washington has published in its Proceedings some 680 papers concerning birds. Separates are still available for most of these and subsequent papers, and are being offered at 5¢ per page (Xerox copies supplied for the few titles not in print). A great many original descriptions of new taxa are found in these papers. A Xeroxed list of titles on Aves is available for $5.20. All orders or inquiries should be addressed to the Treasurer, Biological Society of Washington, National Museum of Natural History, Washington, D. C. 20560.

REQUESTS FOR ASSISTANCE

Shorebird color-marking.—In 1975, the Canadian Wildlife Service plans to carry out extensive banding and color-marking of shorebirds in James Bay and the Maritime Provinces in eastern Canada. Colored leg bands and feather dyes will be used to mark the birds. Observers throughout eastern North America are asked to look out for any such birds and to record details of: species, place, date, details of color marks or bands—for colored and standard metal leg bands record which leg the bands were on, the colors involved, and the relative position of the bands if more than one was on a leg (e.g. right leg, red above blue, etc.). For color-dyed birds, record the color and area of the bird that was dyed. Details should be sent to Dr. R. I. G. Morrison, Canadian Wildlife Service, 2721 Highway 31, Ottawa, Ontario, Canada, K1A 0H3.

International shorebird surveys.—In 1974, shorebird survey schemes were initiated in the Maritime Provinces of eastern Canada and in areas of the eastern U.S. and have provided valuable information concerning shorebird migration and for identifying and documenting areas of major importance. In 1975 it is planned to extend this scheme to as many areas as possible including eastern Canada and the U.S.A., the Caribbean Islands and northern South America. Observers who might be able to participate in regular census surveys during spring and autumn migration periods, as well as in areas where wintering populations of shorebirds are found, are asked to contact one of the following:

(1) for areas in Canada: Dr. R. I. G. Morrison, Canadian Wildlife Service, 2721 Highway 31, Ottawa, Ontario, Canada, K1A 0H3.

(2) for areas in the U.S.A., Caribbean Islands, and South America: Brian A. Harrington, Manomet Bird Observatory, Manomet, MA 02345.

ERRATUM

In Whitmore's paper in the March 1975 Wilson Bulletin (87:65–74), the third sentence of the caption to Figure 2 (p 71) should read as follows: "Low values on the second axis correspond to the presence of shrubs, whereas high values indicate the absence of shrubs."

ORNITHOLOGICAL LITERATURE

Avian Biology, Volume III. Edited by Donald S. Farner and James R. King. Academic Press, New York. 1973: xx + 573 pp., drawings, charts, photomicrographs, photographs. $40.00.—This third volume of *Avian Biology* lives up to the reputation established by the first 2 volumes. The first chapter is a masterly review of avian reproduction by B. Lofts and R. K. Murton. It gives an overview of reproduction and sets the stage for the following chapters. The authors describe not only the gross anatomy but also the fine structure of the testicular interstitial cells and the Sertoli cells. They emphasize the correlation between structure and function, and indicate the manner in which the function of different reproductive organs has been evaluated. It is particularly important that data from numerous wild species and also from domestic species are used in an attempt to integrate and understand the physiologic mechanisms involved in the regulation of gonadal activity by pituitary and gonadal hormones. The electron micrographs are of very good quality, and the legends are clear, so that a non-expert reader should have no difficulties in interpreting the illustrations or the data presented, or in following the authors' salient arguments. My only regret is that the research of A. H. Meier and his co-workers (Meier, A. H. and R. MacGregor, III. Am. Zool. 12:257–271, 1972; Meier, A. H., D. D. Martin and R. MacGregor, III. Science 173:1240–1243, 1971; Meier, A. H., T. N. Trobec, M. M. Joseph and T. M. John. Proc. Soc. Exp. Biol. Med. 137:408–415, 1971) was not included. His experiments on the importance of the temporal relationships between prolactin and corticosterone for reproductive biology of the White-crowned Sparrow have contributed considerably to our understanding of the regulation of the reproductive cycle of this species.

The chapter on the adenohypophysis by A. Tixier-Vidal and B. K. Follett is a valuable contribution to an understanding of the correlation between the morphological features of the pituitary cells and the function and hormonal secretions of these cells. An extensive table listing the responses of different pituitary cells to various stains is especially welcome. This table plus a well produced color illustration and the excellent electron micrographs of the various cells provide details of the morphology. The authors then present the conclusions that may be drawn from the available evidence concerning the morphology and physiology of the pituitary cells, being extremely careful to point out the tentative nature of these conclusions. Comparative endocrinologists and many avian biologists will find this chapter a "must" especially because of the critical review and evaluation of assay methods that have been and are being used to measure hormone content of the pituitary.

The third chapter, "The Peripheral Endocrine Organs," by I. Assenmacher, presents a thorough and scholarly review of the function of the adrenal cortical tissue, adrenal medullary tissue, the thyroid, the endocrine pancreas, the parathyroids, the ultimobranchial bodies, the thymus, and the bursa of Fabricius. The sections on the adrenal and the thyroid bring together a great deal of information, including a wealth of important material from Assenmacher's own laboratory. I regret that the fascinating research by R. K. Cole and his co-workers (Cole, R. K., J. H. Kite, Jr., and E. Witebsky. Science 160:1357–1358, 1968; Cole, R. K., J. H. Kite, Jr., G. Wick, and E. Witebsky. Poult. Sci. 49:839–848, 1970) on hereditary auto-immune thyroiditis in chickens, and the role of the bursa of Fabricius in this syndrome is not mentioned. This work shows the importance of the bursa in forming the auto-immune antibodies to thyroidal tissue. This thyroiditis in chickens in many aspects resembles Hashimoto's disease in man.

H. Kobayashi and M. Wada wrote the chapter on neuroendocrinology, beginning with a review of the morphology of the neurosecretory system. The gross morphology, microscopic, and fine structures are illustrated with well selected drawings, photomicrographs, and electron micrographs. The authors then present the experimental evidence concerning the hypothalamic regions and the releasing factors involved in regulation of the secretion of the various pituitary hormones.

This reviewer lacks expertise to review critically the chapters on sensory reception, but it is evident that they are written clearly and in such a manner that the important features can be understood by non-experts.

In the chapter on vision, A. J. Sillman discusses the morphology of the avian fovea and its relationship to visual acuity. Apparently birds do not have a much greater visual acuity than monkeys and man, but they can perceive a sharp image of an object extrafoveally; this allows them to keep a moving object in sight more easily than humans do. The function of the oil droplets in the retina and the function of the pecten are treated dispassionately. Both seem to remain enigmatic.

B. M. Wenzel reviews chemoreception from anatomical, neurophysiological, and behavioral points of view. A great deal of research on this avian sensory function is yet needed.

J. Schwartzkopff's chapter on mechanoreception has numerous excellent diagrams and illustrations to help explain the morphology and the physiology of the mechanoreceptors, chiefly the auditory organ. The organ of equilibrium and skin sensory receptors and proprioreceptors are also reviewed.

The final chapter, on behavior, by R. A. Hinde covers a wide range of topics, including "learning," in a systematic fashion. Hinde first analyzes animal behavior by describing and classifying different types of behavior, and then illustrating several functional aspects of avian behavior.

My criticism of this volume does not pertain to its quality; on the contrary, it is my opinion that the chapters are all excellent and clearly written. I am impressed by the coverage of the world literature. The flaw is that the arrangement of the chapters in different volumes of the series makes them somewhat dissociated. I think that it would have been more desirable to have one volume which contained the following chapters (possibly in the order indicated): "Neuroendocrinology in Birds," "The Adenohypophysis," "The Peripheral Endocrine Glands," "Reproduction in Birds," "Ecological Aspects of Periodic Reproduction" (by K. Immelmann, published in Vol. 1), "Ecological Aspects of Reproduction" (by M. L. Cody, published in Vol. 1), "Behavior," and "Ecological Aspects of Behavior" (by G. Orians, published in Vol. 1).

Such an arrangement would benefit the readers and buyers of these rather expensive books, although it is a matter of opinion whether another reader would prefer the same grouping of chapters. The selection of chapters for each volume is probably dictated more by the extent to which authors meet deadlines and by the economics of the publishing business than by the judgements and best laid plans of the editors.—Ari van Tienhoven.

Productivity, Population Dynamics and Systematics of Granivorous Birds. Edited by S. C. Kendeigh and J. Pinowski. PWN—Polish Scientific Publishers, Warszawa, 1973: 410 pp., graphs, diagrams, paperbound. Price not given. (Available from Jan Pinowski, Institute of Ecology, Polish Academy of Sciences, Nowy Swiat 72, Warsaw, Poland).—Some 10 years ago Dr. J. Pinowski of the Polish Academy of Sciences, an

active worker on the breeding biology of *Passer domesticus* and *P. montanus*, began to investigate the possibility of setting up a cooperative international program of research into these 2 widely distributed species. Opportunity was taken to discuss this project at the 14th International Ornithological Congress in 1966 and a Working Group on Granivorous Birds was set up under the auspiees of the International Biological Program. The primary aim was to obtain a measure of the importance of granivorous birds in the flow of energy through the agrieultural eeosystem created by man. The genus *Passer* was selected as the most suitable group for these studies, both beeause of the close assoeiation of many of the species of this genus with man and also because of the wide dispersion of the genus throughout the world.

Largely through the enthusiasm of Dr. Pinowski the Working Group attraeted the interest of over 100 individuals and it was possible to hold a special 3-day meeting in 1970 immediately following the 14th International Ornithologieal Congress. This book eontains 25 papers presented at this meeting (2 in summary only) and 6 later submitted papers. Three papers are in French and the remainder in English.

The papers are grouped in 4 principal sections dealing with biometries and bioenergetics, population dynamics, food, and systematics and evolution, with a miseellaneous section for papers that did not fit into the more specific themes. This is always a problem in a general conferenee, but one would have thought that with a meeting of this type a more rigorous seleetion proeedure might have limited papers to the chosen theme. Twenty-four of the papers deal exelusively or principally with *Passer* and the publication would have been improved if it had been restrieted to these papers and a more suitable title chosen. The one chosen is rather misleading because it gives an inaccurate impression of the scope of the papers ineluded. The bulk of the publication deals with *Passer domesticus*, which, as Dr. Kendeigh remarks in his opening address, is well on its way to becoming for ornithologists what the laboratory mouse or white rat is to the physiologist and the fruit fly, *Drosophila*, is to the genetieist.

The first section presents a mass of quantitative data on body weight, covering both growth rates of nestling *P. domesticus* and *P. montanus* in Poland, and daily and seasonal variations in the weight of *P. domesticus* trapped in England. Of partieular interest are data on daily weight in individuals of the migratory raee *P. d. bactrianus* on spring and autumn passage in Tadjikistan. This paper is mainly coneerned with variations in the body make up with respeet to water, fat, and non-fat materials, and shows that adaptations similar to those in other small passerine migrants have evolved in this race of House Sparrow with premigratory weight inereases of up to 6.5 g (ea. 25% of body weight), and the storing both of fat and water to provide energy and compensation for water loss when migrating over arid areas. It is a pity that more of the data in this interesting paper were not presented in tabular form to allow more ready comparison with data from non-migratory populations.

Three of the papers deal with energy requirements. Myreha, Pinowski, and Tomek provide data on nestling *P. domesticus* and *P. montanus* in central Poland (52° N), while Weiner gives results on both cage and aviary studies of the former speeies in southern Poland (50° N). Latitude and longitude readings are transposed in the text.

Weiner's results basieally eonfirm those of earlier workers. An interesting feature is that the energy consumption of aviary birds, which might be expected to exeeed that of caged birds to finanee the cost of free flying, in fact did so only at ambient temperatures above 5° C. Weiner accounts for this by suggesting that the aviary birds clustered together at night, employing "social thermoregulation" to save energy. It was reported

at the meeting that social roosting among wild sparrows was frequent in Poland, where winter temperatures of –20° C are common.

Kendeigh attempts to provide a complete annual energy budget for House Sparrows living in central Illinois (40° N). This is based on considerable experimental work on caged birds carried out over many years, largely by Kendeigh and his collaborators, supplemented with existence requirements data derived mainly from other species and converted weight-for-weight to House Sparrows. Kendeigh acknowledges the limitations of many of the assumptions that had to be made, but nevertheless this is an important paper giving a basis for studying the annual energy requirements of the species, and, by providing full derivations of the different components, suitable conversions can be made to suit localities in different climatic conditions. Factors are given to convert the energy requirements into food, though these are based on laboratory food rather than on foods actually taken in the wild. An important result is the monthly productive energy available over that which is normally used. Providing there is no limitation in food availability, this could determine the range of the species at high latitudes by increased heat requirement to maintain body temperature, and at low latitudes by the inability to realize this potential through heat stress.

The final paper in this section deals with the growth of 7 ground-nesting passerine birds in the Canadian prairie.

The second section is mainly concerned with population dynamics. Eight of the 10 papers deal with *Passer domesticus* and provide breeding data from New Zealand, India, Pakistan, Poland, and the U.S., with one paper from France giving preliminary data on the structure of a population based on the capture and recapture of banded birds. Thus these papers cover geographically, latitudinally, and climatically a representative selection of the House Sparrow's range. Another paper gives similar data for *P. melanurus*, a species indigenous to South Africa. Although *P. melanurus* is associated with man, it is not as closely dependent as *P. domesticus* and the data in this paper, although admittedly from rather atypical Cape Sparrows nesting gregariously in a wine growing area, nevertheless are valuable in providing information for comparison with the better studied *P. domesticus* and *P. montanus*. *P. domesticus* was introduced into South Africa at the end of the last century but only in the last decade or so has it spread over the area and come into significant contact with *P. melanurus*. It will be very interesting to have some information on the interplay between these species, such as already exists for *P. domesticus* and *P. montanus*.

The remaining paper in this section is concerned with census methods for determining the population density of *Agelaius phoeniceus* in the Lake Erie border of the U.S. and Canada. While somewhat off the main *Passer* theme of the conference, it does emphasize the one area that appears to have received somewhat less attention in the *Passer* studies, namely population density and its seasonal variation in different habitats and different parts of the world, though in several of the papers sufficient information is given for this to be extracted. This paper, by Dyer, Siniff, Curtis, and Webb, illustrates very nicely the preferred wetland habitat of this species and emphasizes the considerable variation in numbers that occurs in less favored habitats compared to preferred ones.

Perhaps the greatest value of this section is the full amount of tabular data. This does not make for exciting reading, but does provide in the case of *P. domesticus* a most useful source of data which in due course should allow a much more accurate picture of the species to be built up as well as show how one species can adapt to widely differing conditions.

The section on food contains 2 papers that deal directly with investigations on the food of *P. domesticus* and *P. montanus*. One, based on stomach analyses, gives data on the food taken by these species in the winter in Hesse, West Germany. The other gives preliminary results on seed preference by caged *P. montanus*, but is rather inconclusive. A further paper in this group deals with the food taken by 5 species of dove in Senegal and shows that although there is overlap in the food seed species taken when these are plentiful, the different birds tend to specialize in time of shortage.

Many *Passer* species are agricultural pests and thus are of economic importance. "Economic ornithology" is beset with emotional overtones, but except for the paper by Palmer on *Carpodacus mexicanus* and *Sturnus vulgaris* in California, the economic importance of the birds is not dealt with directly. This paper is really out of place in this publication.

A notable characteristic of the House Sparrow is its sedentary nature over most of its range. It is thus an excellent subject for the study of regional variation and to test adaptation to local conditions. Nordmeyer, Oelke, and Plagemann do this for 5 populations of *P. domesticus* from different parts of West Germany using external measurements. Johnston and Selander compare some 40 North American populations using principally skeletal characters. The latter supports the earlier results of these workers in showing that adaptive evolution has taken place in the 110–120 years since the species was introduced to North America. Significant variations are demonstrated for both areas and where the data are appropriate, appear to support the Allen and Bergmann "rules." A third paper in the "systematics" section by Rising examines House Sparrows taken from Kansas in the autumn and spring, and shows variations that can be explained by selection to the winter climate that are consistent with the variations for a sedentary species shown in the 2 previously discussed papers.

Johnston and Selander are prepared to regard *P. domesticus* and *P. hispaniolensis* and their intermediates as belonging to a conspecific complex (though the large area where the 2 are sympatric but do not interbreed presents considerable difficulty in accepting this view) and in this context the paper by Bortoli on sparrows in Tunisia would have been more appropriately located in this section than in the one on food. This is an area of much interest for those concerned with *Passer* systematics. Although the Tunisian birds can be allocated to *hispaniolensis*, Bortoli reports that hybrid *domesticus* × *hispaniolensis* types, as defined by male plumage characteristics, appear to be evolving ecologically as "*domesticus*" by associating closely with man and remaining sedentary in contrast to the seasonal movements of the typical *hispaniolensis* birds. This would seem to be based on a genetic penetration of *domesticus* from the west through interbreeding.

The "miscellaneous" section includes 3 papers on *Passer* species concerned with pathology and physiology. In separate papers Martin studies the influence of dietary protein on the low temperature tolerance of *P. domesticus* (and the American Tree Sparrow, *Spizella arborea*), and in collaboration with Votava the effect of low partial pressures of oxygen on the House Sparrow. If the oxygen pressure is translated into the equivalent altitude it would appear that the House Sparrow should be able to survive at 6000 m. Natural populations are in fact found up to 5000 m in the Himalayas. Bont and Franssen artificially infected caged specimens of *Passer griseus* with *Salmonella* after finding infected wild individuals and studied the effect on the blood plasma proteins. The results obtained were influenced by the birds becoming simultaneously infected by *Coccidium*.

This publication will be valuable to those interested in the genus *Passer* rather than for the wider field suggested by the title. It is mainly a collection of basic data. The synthesis is promised in a further volume now in preparation by the editors following

a second meeting of the Working Group in Warsaw in September 1973. The editors and publishers, printing in a foreign language, are to be congratulated on the almost complete absence of spelling and printing mistakes.—J. Denis Summers-Smith.

Feathers in the Wind—the Mountain and the Migration. By James J. Brett and Alexander C. Nagy. Hawk Mountain Sanctuary Association, Kempton Pennsylvania, 1973: 72 pp., 13 photographs, 5 in color including cover, numerous drawings, diagrams and maps. Paper cover. $2.25.—The art of identifying flying hawks has advanced enormously since the early years at Hawk Mountain and this new publication by staff members of the Hawk Mountain Sanctuary should be an invaluable aid not only to the beginner but to most experienced hawkwatchers. The hawk-by-hawk descriptions contain much helpful information not found elsewhere, and gleaned personally by incomparably long hours on the mountain. Each species account is illustrated by a number of drawings showing various flight aspects and anatomical features . . . a long step forward from the usual single figure in a field guide.

Although the chapter on identification is perhaps the most useful feature, other chapters include a short history of the Sanctuary (just a reminder of Dr. Broun's classic of 25 years earlier), the topography of Hawk Mountain, the geography of this and other hawk migration observation points (but no indication of the patterns of the spectacular spring flights through parts of the Great Lakes system), some aerodynamic principles and weather patterns conditioning hawk flights, a reminder of hawk shooting, a bit about DDT, and ancillary material including a yearly summary from 1934 through 1972. If the statement: "As a result of the Sanctuary's educational endeavors, all species of hawks, eagles and owls are now protected by law" seems somewhat sweeping, no one will dispute the Sanctuary's place as probably the major influence in a generation's turn-about in its view of hawks. Fortunately this small volume will fit a coat pocket along with other field guides.—Walter R. Spofford.

The Dell Encyclopedia of Birds. By Bertel Bruun. Dell Publishing Co., Inc., New York, 1974: 240 pp., 395 color illustrations. Paper cover. $2.45.—This is a handy collection of over 641 ornithological terms and biographical entries briefly defined and listed in alphabetical order. The more than 395 color paintings by Paul Singer are adequate but uninspired, and the anatomical drawings contain several minor errors. The text entries, on the other hand, are accurate and concise.—R. J. R.

Index Ornithologorum. The Ring, vol. VI. By W. Rydzewski (ed.). Polish Zoological Society, 1972: iv + 112 pp. Paper cover. $3.00. Order from: Editor of The Ring, Sienkiewicza 21, 50-335 Wroclaw, Poland. Checks should be made out to "Polish Zoological Society."—Here is a very useful list of ornithologists of the world, and a great aid in finding persons in various countries sharing one's interests. In a Personal Index the names are listed alphabetically according to country, and for each the following information is provided: surname, other names, year of birth, title, occupation or situation, memberships in principal ornithological organizations, editorships, principal interests in ornithology, address. This is followed by a Subject Index in which the names are listed referring to the Personal Index.— R. J. R.

CONSERVATION SECTION

CONSERVATION COMMITTEE REPORT ON STATUS OF SANDHILL CRANES

Sandhill Cranes (*Grus canadensis*) historically occurred in many areas of North America and eastern Siberia. In North America they occurred from the arctic tundra and boreal forest on the north to the coastal marshes and river basins of the southeast, south, southwest and far west. Six subspecies of Sandhill Cranes have been described and recognized by some authorities. These are: the Lesser (*G. c. canadensis*) nesting in tundra and boreal areas of Siberia and northern North America, the Canadian (*G. c. rowani*) which nests in central Canada, the Greater (*G. c. tabida*) nesting in the Lake States and northwestern North America, the Mississippi (*G. c. pulla*) in Mississippi, the Florida (*G. c. pratensis*) in Florida and Georgia, and the Cuban (*G. c. nesiotes*) in Cuba. Reliable data on status of populations prior to the advent of settlement are lacking but cranes were undoubtedly more numerous at that time. With the advent of white settlement cranes were hunted for food and many favored habitats were drained for agriculture with resultant adverse effects on crane numbers.

Due to vastness of occupied breeding habitats, wariness of cranes and low levels of sportsmen interest, few detailed regional studies of cranes were made until the mid-1960's. Presently, interest and research on Sandhill Cranes has intensified with studies being accomplished on the Greater, Mississippi and Florida subspecies. Unfortunately, little effort has been expended on the two subspecies, Lesser and Canadian, which are subjected to hunting. Because of the lack of data on these two races and concern about the endangered Whooping Crane (*Grus americana*) which migrates through areas open to Sandhill Crane hunting, some authorities have written about the possible threat of hunting to Sandhill and Whooping Crane populations. It is important to recognize that Sandhill Cranes have inherently low productivity as average clutches contain two eggs and adults apparently do not reach maturity until three years or older. Annual recruitment is not accurately known although studies of hunted and non-hunted migratory populations indicate that from 4 to 37% of cranes in fall flocks and in game bag checks are young of the year. Thus, concern has been expressed about hunting of cranes because of their low productivity and the overall lack of data on population trends and harvest rates. These concerns are justified. Because of the expressed concerns about the future of Sandhill Cranes, the Conservation Committee of The Wilson Ornithological Society initiated this review to better understand the problems associated with crane management. The basic problems encountered are:

(1) No specific management plan has been prepared for Sandhill Cranes by state and federal agencies. (2) Reliable estimates of breeding populations, productivity and recruitment to fall populations are not presently available for the hunted Lesser and Canadian subspecies. (3) Adequate estimates of hunter harvest and crippling loss are largely unavailable for most areas. (4) Breeding and wintering habitat available to cranes will undoubtedly continue to decrease in quality and quantity.

HISTORY OF SANDHILL CRANE HUNTING

A general hunting closure on all cranes was invoked in the U.S. in 1916 and remained in effect until January 1961 when a 30-day season was opened on the Lesser (Little

Brown) Sandhill Crane in eastern New Mexico. The first open season was prompted by requests from the Central Flyway Waterfowl Council because the Lesser subspecies (including Lesser and Canadian) were believed to be sufficiently abundant, and they were causing considerable localized depredations to unharvested grain crops, mainly during fall migration on the northern plains of the U.S. and in the prairie provinces of Canada. Due to severe losses of grain crops in Saskatchewan, officials authorized the shooting of Sandhill Cranes under general crop depredation orders in 1959. A second hunting season in the U.S. was permitted during the fall of 1961 and was expanded to include west Texas and Alaska.

Between 1967–1972, six additional states, all in the Central Flyway, were permitted to open specified areas to hunting. Sandhill Cranes have been hunted in Mexico for years. In Canada, seasons have been allowed in Saskatchewan and Manitoba since 1964.

Studies conducted by the Bureau of Sport Fisheries and Wildlife and New Mexico Department of Game and Fish prior to the initial 1961 open season indicated that neither the scarce Greater Sandhill Crane nor the endangered Whooping Crane would be influenced by a hunting season in eastern New Mexico or west Texas. Hunting seasons in other Central Flyway States were deferred until completion of a 4-year study which obtained considerable information about cranes, including localities frequented by the Greater subspecies and the relationship between the fall migration chronology of Sandhill and Whooping Cranes.

These studies showed that the fall migration of Whooping Cranes is rather predictable. Whooping Crane sightings were reported at Sandhill Crane fall concentration sites in Saskatchewan, northeastern Montana, North and South Dakota, Kansas and northern Oklahoma. In contrast, Whoopers were not observed at Sandhill Crane concentration areas in northcentral Montana, southeastern Wyoming, eastern Colorado, or western Oklahoma. Likewise, the two species were not observed together after November 8 anywhere in the Central Flyway north of Texas.

Present crane hunting season dates in the Dakotas and Oklahoma take into consideration the migration chronology of Whoopers. Where Whoopers are likely to occur in company with Sandhills, opening dates are delayed until after early November. In addition, measures are available to close the season in any locality where Whoopers appear during a Sandhill Crane season.

These same studies have also shown that hunting has little or no impact on populations of the Greater Sandhill Crane since none or very few occur in areas with open seasons. While a small portion of the cranes present during early fall in Kidder and Pierce counties, North Dakota, are the Greater subspecies, it is doubtful if hunting threatens the Greater subspecies in North Dakota as the season opens in November after most cranes of all subspecies have departed and only a few birds are generally harvested (estimated harvests ranged from none in 1971 to 400 in 1970). Further, recent studies throughout the U.S. show that the Greater subspecies is more numerous than previously believed and that most populations are presently increasing.

Available data indicate that present crane hunting seasons in the U.S. do not threaten the less common Greater subspecies and seasons are manipulated to reduce the possibility of jeopardizing Whooping Cranes. However, the mistaken shooting of even one Whooper cannot be overlooked. To date, such a mistake is not known to have occurred in any areas open to the hunting of Sandhill Cranes.

Since present seasons do not appear to threaten either the Greater subspecies or the Whooper, the question may be asked what impact has hunting had upon crane populations subject to harvest? Justifications for open seasons were based primarily upon a

population of some 200,000 Lesser and Canadian Sandhills which managers believed could sustain a limited harvest and at the same time hunting could reduce local crop depredations through dispersal of birds from areas receiving damage. These justifications appear to be reasonable.

Requests for open seasons prompted the initiation of several studies by management agencies including an evaluation of the first hunt in New Mexico, limited banding projects in New Mexico and Nebraska and a survey of Central Flyway crane populations. Except for the evaluation of the first New Mexico hunt, however, only scanty information has been obtained on the impact of hunting on Sandhill Cranes. Available data collected since 1961 are insufficient and population responses to hunting and reduction in crop depredations cannot be adequately evaluated.

Data are lacking to accurately assess hunting pressure and harvest in North America. Presently, four states (Alaska, Colorado, New Mexico, North Dakota) and Canada obtain estimates of crane harvests by questionnaire while other states make estimates of harvest or have no information. Even where harvest questionnaires are employed, they are not specifically designed to sample crane hunting. Instead, estimates are obtained from general harvest questionnaires for waterfowl or all game birds. Thus, sample sizes are inadequate and do not provide accurate estimates of hunter participation and kill for lightly hunted species like cranes. The total annual harvest for North America, including adjustments for crippling loss, harvest in Mexico, Siberia and by natives in Canada and Alaska may approach 15,000 cranes. This figure, however, is mainly conjecture and provides only a crude estimate.

PRESENT STATUS OF SANDHILL CRANES

Lesser Sandhill Crane.—This subspecies nests in arctic and subarctic regions from Siberia to the west shore of Hudson Bay and winters in Texas, New Mexico, southeastern Arizona, and Mexico. Most population surveys have been taken during spring along the Platte River in central Nebraska. An estimated peak population of 200,000 Lesser and Canadian Sandhill Cranes are present in that area during most springs in recent years. Since several thousand Lessers have probably moved further north or have not arrived on the Platte River, counts are minimal. An additional 20,000 Lessers migrate through the Pacific states and winter in the California Central Valley and Carissa Plains. At the minimum, there are an estimated 250,000 to 280,000 Lesser Sandhill Cranes. This population appears to be relatively stable.

Canadian Sandhill Crane.—This race nests from Ontario to west-central British Columbia and is presumed to winter in coastal Texas and Mexico. No reliable estimates are available as to the size of this population but best guesses are that they number from 15,000 to 20,000. Little knowledge exists about this subspecies and it is not known whether they are increasing or decreasing.

Greater Sandhill Crane.—Four populations of this race are presently recognized. These are: (1) *Eastern*—This group nests from Michigan, Minnesota, Wisconsin, southeastern Manitoba to southwestern Ontario and winters in southern Georgia and and Florida. The population is estimated at 7,000 birds and they are presently increasing. (2) *Rocky Mountain*—The nesting area is in eastern Idaho, western Wyoming, northeastern Utah, southwestern Montana, and northwestern Colorado, and they winter in western New Mexico, northern Mexico, and southeastern Arizona. At present the population is increasing with an estimated 10,000 to 15,000 individuals. (3) *Colorado River Valley*—The Colorado River Valley population nests in northeastern Nevada and probably southcentral Idaho, and winters primarily south of Parker, Arizona, and near

Brawley, California. Their estimated number is 1,000 and present status is unknown. (4) *Central Valley*—This population nests in southcentral and southeastern Oregon and northeastern California with an additional segment of about 300 birds nesting in southern British Columbia. They winter in the California Central Valley from Chico to Delano. Presently this population appears stable, with an estimated 3,500 birds.

Mississippi Sandhill Crane.—This subspecies occurs only in Jackson Co., Mississippi and there are an estimated 38 to 40 birds in the population. At present they are stable to decreasing. With increased human encroachment and highway development, the subspecies is in danger of becoming extinct in the very near future unless a refuge is established.

Florida Sandhill Crane.—Presently there are an estimated 5,200 Florida Sandhill Cranes ranging from the Florida Everglades to Okefenokee Swamp, Georgia. Currently the subspecies is increasing as new habitat becomes available from clearing, fencing, and grazing. However, with increased real estate and U.S. Corps of Engineers developments the population will probably decrease as additional habitat is destroyed.

Cuban Sandhill Crane.—This subspecies is endemic to western Cuba and the Isle of Pines. The present status of the population is unknown. Estimates in the early 1950's put this population at 100 birds. Recent evidence indicates that the population is holding its own.

Current estimates indicate there are from 285,000 to 320,000 Sandhill Cranes if all races are considered. At least 265,000 of these are in the two races (Lesser and Canadian) which are hunted. For specific detailed data from which this report was prepared, contact Dr. C. E. Braun, Wildlife Research Center, P.O. Box 2287, Ft. Collins, CO 80521.

SUMMARY

Sandhill Cranes occur throughout much of North America, with one subspecies extending into Siberia and another isolated in Cuba. Six subspecies are described, with the three migratory races (Lesser, Greater and Canadian) being the largest numerically. The three non-migratory races (Florida, Cuban and Mississippi) are local in distribution with only the Florida subspecies consisting of more than a few hundred individuals. Presently 285,000 to 320,000 Sandhill Cranes exist, with most (265,000) being in two races, Lesser and Canadian. These two races are the only ones hunted legally in the U.S., Canada and Russia. In Mexico, all Sandhill Cranes may be hunted. Hunting of cranes for sport was initiated in 1961 and it is estimated that the total annual harvest including crippling loss could approach 15,000 birds. Recently, concern has been expressed about the potential for overharvest of Sandhill Crane populations presently being hunted and with the fate of the endangered Whooping Cranes that migrate through areas open to hunting. No documentation exists that Whooping Cranes have been mistaken for Sandhill Cranes in areas open to hunting of the latter species. Major problems associated with Sandhill Cranes relate to lack of overall management goals, lack of reliable population, recruitment and harvest data for the two hunted races, and continued deterioration of breeding and wintering habitats due to man's activities. The best data available indicate that two subspecies are increasing (Greater and Florida), three are stable (Lesser, Canadian and Cuban) while one population (Mississippi) is in danger of extinction.

RECOMMENDATIONS

1. Spring population surveys of the hunted Lesser and Canadian subspecies should be intensified and improved not only along the North Platte River in Nebraska

but both north and south of this staging area. Surveys in all areas should be conducted simultaneously in order to avoid duplications and to arrive at a more reliable population estimate.

2. Estimates of annual recruitment in hunted Sandhill Crane populations through systematic counts of adults and immatures by trained and interested personnel should be conducted annually during fall and early winter (October–December) in all major fall concentration and wintering areas.
3. Efforts should be made to obtain better estimates of harvest, crippling loss, and hunter participation in all states, provinces and countries having hunting seasons. This should be accomplished through requiring all hunters to have a special permit for crane hunting.
4. Efforts should be initiated to band representative samples of cranes in wintering and/or staging areas in order to assess hunting pressure, mortality rates and geographical distribution of the harvest.
5. No expansion of crane hunting should be allowed until sufficient biological data are available to support such a decision. Indeed, if improved census and harvest data become available, it may be necessary to restrict crane hunting in some areas or on some populations or subpopulations.
6. Federal and state agencies concerned with management of cranes should prepare a long term plan for the perpetuation and enhancement of the species.
7. In areas where crop depredations are severe, efforts to disperse cranes through methods other than hunting should be increased and monetary reimbursement to landowners with damage by cranes should be considered.
8. Federal and state agencies should be encouraged to continue identifying and protecting crane nesting areas.
9. Every effort should be made to monitor the fall migration of Whooping Cranes. If they are jeopardized by the hunting of Sandhill Cranes, such localities where conflict exists should be closed to all crane hunting.
10. Establishment of a refuge for migrating Sandhill Cranes in the Great Bend area of the Platte River, Nebraska as proposed by the U.S. Fish and Wildlife Service is an important step in crane management. The Wilson Ornithological Society supports the establishment of such a refuge as early as feasible.

ACKNOWLEDGMENTS

Personnel of state and federal conservation agencies greatly facilitated the preparation of this report by unselfishly providing access to unpublished reports. The cooperation of these individuals and their agencies is appreciated.

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Conservation Committee
R. C. Drewien
C. D. Littlefield
L. H. Walkinshaw
C. E. Braun, Chairman

Editor's Note: Definite plans have now been made for the establishment of a National Wildlife Refuge in Jackson Co., Mississippi for the protection of the Mississippi Sandhill Crane. Plans are also continuing to construct U.S. Interstate Highway 10 through the crane breeding area.

This issue of *The Wilson Bulletin* was published on 30 May 1975.

THE WILSON BULLETIN

Editor JEROME A. JACKSON
Department of Zoology
P.O. Drawer Z
Mississippi State University
Mississippi State, MS 39762

Editorial Assistants ROBERT J. ESHER
DAVID F. WERSCHKUL

Review Editor ROBERT RAIKOW
Department of Biology
University of Pittsburgh
Pittsburgh, PA 15213

Color Plate Editor WILLIAM A. LUNK
865 North Wagner Road
Ann Arbor, MI 48103

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The Wilson Bulletin

PUBLISHED BY THE WILSON ORNITHOLOGICAL SOCIETY

VOL. 87, NO. 3 SEPTEMBER 1975 PAGES 303–440

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THE WILSON BULLETIN

The official organ of the Wilson Ornithological Society, published quarterly, in March, June, September, and December. The subscription price, both in the United States and elsewhere, is $10.00 per year. Single copies, $2.50. Subscriptions, changes of address and claims for undelivered copies should be sent to the Treasurer. Most back issues of the *Bulletin* are available (at $2.50 each) and may be ordered from the Treasurer. Special prices will be quoted for quantity orders.

All articles and communications for publications, books and publications for reviews should be addressed to the Editor. Exchanges should be addressed to The Josselyn Van Tyne Memorial Library, Museum of Zoology, Ann Arbor, Michigan. Known office of publication: Department of Zoology, Mississippi State University, Mississippi State, Mississippi 39762.

Second class postage paid at Mississippi State, Mississippi and at additional mailing office.

PRINTED IN U.S.A. Allen Press, Inc., Lawrence, Kansas 66044

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Chick and nest of the Marbled Murrelet *(Brachyramphus marmoratus marmoratus)* from Big Basin Redwoods State Park, Santa Cruz Co., California. Live chick photographed on 8 August 1974. Nest (as seen from above) on portion of horizontal limb after removal from tree; much of whitish ring of droppings missing; moss beyond brown ring was a much brighter green in life. From Kodachrome II transparencies.

THE WILSON BULLETIN

A QUARTERLY MAGAZINE OF ORNITHOLOGY

Published by the Wilson Ornithological Society

VOL. 87, NO. 3 SEPTEMBER 1975 PAGES 303–440

DISCOVERY OF A NEST AND THE DOWNY YOUNG OF THE MARBLED MURRELET

LAURENCE C. BINFORD, BRUCE G. ELLIOTT, AND STEVEN W. SINGER

On the afternoon of 7 August 1974, Hoyt Foster, a tree surgeon for the Davey Tree Company, was removing branches from a large Douglas-fir (*Pseudotsuga menziesii*) in the Santa Cruz Mountains of coastal California. As Foster reached a limb high above the ground, he beheld the first North American nest and the only known downy chick of the Marbled Murrelet (*Brachyramphus marmoratus*). This discovery brought to a conclusion a search that has captured the imagination of North American ornithologists for 185 years (for partial historical summaries see Bent 1919, Guiguet 1956, Drent and Guiguet 1961, Sealy 1972 and 1974).

In this report we describe the nest, eggshell fragments, and nestling, all of which are now in the California Academy of Sciences (CAS), and discuss their bearing on the breeding biology and taxonomy of the species. Additional details of the circumstances surrounding this discovery have been published by Singer and Verardo (1975). The subspecies concerned here is *B. m. marmoratus*, which summers primarily from Kodiak Island, Alaska, south through the northern half of coastal California (A. O. U. 1957). Kuzyakin (1963) presents a well-documented account of a Siberian nest of the Palearctic race, *B. m. perdix* (see Discussion).

Locality.—The nest tree overshadows campsite J-1 at an elevation of about 310 m in Big Basin Redwoods State Park, Santa Cruz Co., California. The campsite is about 27 km northwest of the city of Santa Cruz and 10 km due northeast of the nearest point on the Pacific coast, the mouth of Elliot Creek on Año Nuevo Bay.

Marbled Murrelets are known to feed throughout the year in this portion of the Bay, as well as at Pigeon Point, 15 km west of the nest site. On 18 and 19 May 1914 Dawson (1923) saw a number of Marbled Murrelets flying down-valley along "Major Creek" (= Big Creek) on the slopes of Ben Lomond, a mountain southeast of Big Basin Redwoods State Park. Within

FIG. 1. Marbled Murrelet nest tree and surrounding habitat, Big Basin Redwoods State Park, Santa Cruz Co., California. Arrow indicates point where nest limb, which projected to the south (right), was removed. Photo taken by S. A. Mitchell on 10 January 1975.

Big Basin flying adults were noted on 19 April and in July 1959, and a live juvenile nearly devoid of natal down was discovered on the forest floor on 9 September 1974 (Singer and Verardo 1975). Other grounded juveniles in similar plumage were found in Big Basin on 18 August 1960 and in nearby Portola State Park on 15 June 1957 (Anderson 1972).

Habitat and nest site.—The nest was 45 m above the ground and 6.8 cm from the trunk (to nearest edge of nest bowl) on the broad almost flat top of a limb of a Douglas-fir. The nest tree, 61 m in height (determined by triangulation) and 167 cm in diameter (at 1.2 m), was situated (Fig. 1) amidst a virgin association of generally smaller Douglas-firs and mostly larger coast redwoods (*Sequoia sempervirens*), with a second-story of tanoak (*Lithocarpus densiflorus*), California live oak (*Quercus agrifolia*), and madrone (*Arbutus menziesii*). Within a 26 m radius of the nest tree were 7 other Douglas-firs and 14 coast redwoods, a ratio of 1:2. Beneath the tree, the ground was bare in the campsite and elsewhere densely coverd with a nearly pure growth of California huckleberry (*Vaccinium ovatum*) 1.5 to 2.5 m tall. From ground level the top of the nest tree appeared completely enclosed by branches. At the height of the nest, however, much of the southeast quadrant was open, owing to the lowness of the canopy, and would have provided the murrelets with easy, although not direct, access to the ocean. The vegetation in that direction would have allowed departing birds a 6 m drop within 3 horizontal meters of the trunk and practically unlimited descent beyond.

The nest limb, which measured about 41 cm in diameter at its base and about 15 m long, projected a few degrees west of south and sloped downward very slightly. The presence of a large southward-oriented limb beginning about 180 cm above, together with the slight southward slant of the trunk, provided a sheltering overhang for the nest. Another large branch, directed south-southwest, emerged 132 cm beneath the lower surface of the nest limb. The nest limb was located above a campground, and its distal 5 m was about 60% dead; as a safety precaution this entire limb (and nest), plus several other branches, were removed on 8 August.

Bright green moss (*Isothecium cristatum*) 5 to 10 mm in depth completely coated the upper surface of the basal half of the nest limb but became sparser toward the sunlit tip. When fresh this moss was a much brighter green than indicated in the Frontispiece. A scattering of brown, fallen fir needles and a few sprigs of lichen completed the covering. The only patch of brown moss on the limb was that surrounding the nest. The bark of the trunk was dark brown with scattered reddish brown streaks: it was lightly coated with bright green moss on the north side but virtually bare on the south (nest) side.

Opal Creek, approximately 215 m west of the nest tree, and Blooms Creek, about the same distance south, merge several hundred yards to the southwest to form Waddell Creek, which enters the Pacific Ocean about 10 airline km southwest. In late summer water in Opal and Blooms creeks is reduced to a trickle connecting deeper pools. According to Park records, rainfall occurs almost exclusively in the winter (Nov.–Apr.): from 1 July 1888 through 30 June 1973 the annual (1 July–30 June) average was 133.32 cm and the extremes were 315.62 cm (1889–90) and 51.18 cm (1923–24).

Nest.—Foster made an unsuccessful attempt to obtain photographs of the nest prior to removing the nest limb. Despite the most careful efforts, portions of the nest were lost and others damaged during the strenuous and hazardous task of lowering the limb to the ground. Detailed inspection of the nest, however, permits us to present a reasonably accurate description. The Frontispiece shows the nest as it now exists, i.e. without much of the white ring of droppings.

The nest (CAS 8717) is little more than a depression or "bowl" in the bark, incompletely ringed by droppings. The oblong bowl is lightly whitewashed, devoid of even a vestige of moss, and oriented at a 30° angle (approximately NNE–SSW) to the long axis of the limb. It measures about 9.5 × 6.5 cm, but because the sides turn up at an abrupt angle, the effective size for holding an egg is about 8.0 × 4.5 cm. The thin layers of bark that line the bowl curl up marginally to form small ridges. The bowl appears to be natural, although we cannot discount the possibility that the adults had removed flakes of bark (and adhering moss). There are no apparent bill or claw marks in the wood.

We could find no loose nest material that might have been assembled by the adults. At first the nest rim probably was composed solely of naturally growing moss. Later it was built up in a fortuitous manner through the voiding action of the chick (and perhaps adults) to form a thick "ring" of droppings held together by an underlying meshwork of moss. The ring is broken on the trunk side by a mound of bark 5.0 cm wide (at bowl edge) and covered with brown-tipped moss, which apparently was too high for the nestling to reach with its droppings. Elsewhere the ring varies from 16.5 to 19.5 cm in outer diameter (maximum perpendicular to limb axis) and 4.0 to 7.0 cm in width; the latter variation is a result of the off-center position of the bowl. A few dried needles and twig fragments, in the same frequency as on the remainder of the branch, are scattered under and within the droppings. The upper (more recent) layers of droppings throughout most of the ring have been lost by handling, thus revealing the faintly buffy-white, rather crumbly, lower layers. The few intact portions reach a maximum thickness of about 5 mm (down to the

moss tips) and average about 3.0 cm above the deepest part of the bowl. They demonstrate that the surface of the outer coat was composed of smooth, rounded, slightly glossy hillocks that varied in color from buffy-white to pale Cream-Buff (capitalized colors from Ridgway 1912). The latter color is most prominent in the centers of the hillocks and resembles closely the Pale Ochraceous-Buff of the chick. The underlying moss is in surprisingly good condition: the tips of some plants are brown, but other tips and all bases are dark green, somewhat less bright than the moss away from the nest. Surrounding the ring of droppings is an area of Cinnamon-Buff moss, varying in width from 3.5 to 6.0 cm. Some plants are brown throughout, but most are green basally. The nest gives off a rather strong fishy odor reminiscent of a marine bird colony.

Eggshell fragments.—During the nest recovery approximately 165 fragments of eggshell (CAS 8717), ranging in size from less than a millimeter to 7.1 mm across, were removed from the ring of droppings (mostly from the lower layers) and surrounding moss. Several other pieces remain embedded in the ring. None was found in the bowl. The pieces represent perhaps a third of a shell, but whether they come from more than one egg cannot be determined. In ground color a few fragments are very slightly paler than the others, but this may be due to fading. A few fragments are lined with shell membrane. The absence of yolk and blood suggests normal hatching.

The colors of the fragments agree closely with those ascribed by Sutton and Semple (1941) to an egg taken from the oviduct of a female: Pale Glass Green with spots of Lavender-Gray, Deep Madder Blue, Sepia, Bone Brown, and Black. In addition we noted markings of Saccardo's Umber. The spots range in size from 4 to less than 0.1 mm in diameter.

Nestling.—When first seen the nestling was squatting motionless in the nest bowl and facing northwest toward Foster. It was very reluctant to leave the nest, turning somewhat and shifting up and down when its body was prodded and wings lifted with a pruning saw. It pecked the saw vigorously. When Foster attempted to cover the chick with a shirt, it scuttled quickly backward, toppled off the limb, and fluttered silently to the ground, bouncing and sliding off several other branches on the way and landing 7.5 m south of the trunk. Foster believed that the bird "intentionally" jumped rather than be caught. These actions suggest that the nestling defends itself against predators and leaves the nest only upon great provocation. The speed of fall was described by observers on the ground as like a parachute—about 30 kph; the wings were flapped rapidly.

Apparently unharmed by its fall, the chick was captured and remained in captivity until its death on the evening of 8 August, on which date the

live bird was photographed extensively by Elliott (Frontispiece). The bird appeared very alert and active. It moved quickly with a peculiar and comical waddling gait and demonstrated no aggressive behavior when handled. At no time between its discovery and death did it utter any sound.

When left in direct, late afternoon sunlight for only a minute, the chick began panting and almost immediately moved into nearby shade, where it remained motionless. Foster believed that the nest site would receive several hours of hot direct sunlight in the middle of a typical summer day. During the remainder of the day the site would be in warm filtered light. Early morning fog is sporadic at the site and, in any event, would rarely provide shade during midday because it usually burns off by mid-morning. These observations suggest that during the day a chick of this age can independently maintain its body temperature and hence could be left unbrooded. No adult was seen near the nest. However, Foster had been working in the nest tree for 3½ hours before discovering the nest and probably would not have noticed a departing adult.

The chick, prepared by Binford as a study skin and body alcoholic (both CAS 68895), proved to be a male weighing 95.6 g and possessing testes measuring 3½ × 1 (left) and 2½ × ½ (right) mm. Fat, termed moderate, was restricted to the feather tracts, primarily on the ventral surface of the body, where the feather bases were about half obscured. The digestive tract contained only some partially digested egg, which was fed to the bird during its 24-hour period of captivity, and a few down feathers.

The chick was undergoing complete molt into juvenal plumage. Although the flight feathers are about three-fourths grown and the remainder of the contour feathers almost completely unsheathed, most retain neossoptiles attached to their tips. This nestling down is long, soft, lax, and moderately dense. Average down feather lengths for selected regions are: center of the back, 30 mm; forehead, 5 mm; underparts, 20 mm. Regions of the specimen that lack nestling down are the forecrown, chin, upper throat, cheeks, eyelids, most of the forehead, all but one primary, most upper lesser wing coverts, most upper greater primary coverts, all under wing coverts, and the alular quills. Neossoptiles missing from a small patch on the breast probably were lost during preparation. Some down apparently was lost during captivity, perhaps as a result of handling, since photos (Frontispiece) taken on 8 August show down at the tips of the alular quills and on anterior portions of the head. We can find no evidence that the chick possessed 2 sets of nestling down; the tips of the down feathers seem too long, slender, and tapered (hairlike) to have supported protoptiles.

The unusually late retention of nestling down may function in affording the chick cryptic coloration for as long as possible before fledging: the black-and-white juvenal plumage against the brown and green moss of the nesting limb would be quite conspicuous to predators. The down must also function as insulation and perhaps has been selectively favored over the development of a thick layer of subcutaneous fat in this species that probably must be light enough to fly on young wings directly from the nest site to the ocean.

To determine the degree of development of the chick, we compared its dimensions with the averages of 9 adult males (CAS) taken on 26 March 1907 in Monterey Bay, California. In the following list each chick measurement is presented first, followed in parentheses by the average of the adult males and the percentage of this average that the chick had attained: chord of wing, 93.8 mm (124.3 mm; 75.5%); tail, 24.3 (31.9; 76.2); tarsus, 17.1 (17.7; 96.6); middle toe without claw, 23.3 (24.1; 97.7); culmen from anterior edge of nostril, 11.0 (17.0; 64.7). Chick measurements for the tarsus and middle toe fall between the extremes for adults and hence could represent maximum growth in this individual. The weight of the chick was about 43% of adult weight (loss of weight from unusual exertions, starvation, and freezer desiccation not considered). Newly fledged birds have attained about 70% of adult weight (Sealy 1972). Because growth patterns in the Marbled Murrelet are unknown (Sealy 1972), we cannot estimate the age of the chick.

The underparts posterior to the throat are unpatterned. The individual down feathers of the abdomen are whitish at the base. Pale Smoke Gray medially, and Light Buff at the tip, the combination producing an overall aspect of light buffy-gray. This area blends into the darker buffy-gray sides and flanks, the feathers of which are Pale Smoke Gray at the base, Deep Mouse Gray medially, and Light Ochraceous-Buff at the tip.

The throat and upperparts bear an intricate pattern of deep buff with Sooty Black patches. The buff areas vary from Pale Ochraceous-Buff on the throat to Light Ochraceous-Buff on the upperparts (strongest along the midline of the back). The individual feathers are tipped with either Sooty Black or buff; their basal and medial portions may be Deep Mouse Gray, Sooty Black, Light Buff, or Pale Ochraceous-Buff, in a variety of combinations.

Prior to preparation of the study skin Binford made sketches of the pattern of down on the head and neck (from the bill tip to a point about 90 mm posterior). Because the down is long and loose, delineation of the pattern is difficult and must be treated as approximate until a much younger bird can be acquired. Twenty-seven spots of Sooty Black can be discerned

FIG. 2. Diagrammatic representation showing the distribution of black spots on the anterior portion of the Marbled Murrelet chick. Drawing by Ken Carlson.

(Fig. 2 and Frontispiece): one each on the midlines of the occiput, nape, and upper throat; 2 on each side of the lower throat: and 10 on each side of the head and neck. Because the down is attached to the tips of nearly full-grown contour feathers, the spots appear at first inspection to be located much farther posteriorly than they actually are: all originate from contour feathers anterior to the back and breast. The areas of down now missing from the anterior portions of the head also possessed dark spots, as evidenced by a few remaining tufts and by photos of the live bird. The pattern on the remainder of the upperparts is too intricate to diagram; the area can be described as Light Ochraceous-Buff mottled with a lesser amount of Sooty Black.

Near the tip of each mandible is an egg tooth consisting of a horn-colored area surrounding a single, slightly off-center (toward the bill tip), white bump that is anteroposteriorly oval and highest toward its anterior end. The tooth on the upper mandible measures about 2.5 mm long and that on the lower mandible 1.6. Each is as wide as its respective mandible, but neither reaches the tomium. The lateral edges of both teeth appear chipped, as if they were being lost by fragmentation rather than in toto. The egg teeth are still present in newly fledged chicks (Sealy 1970).

The following notes on "soft part" colors were taken from the photographs and from the fresh specimen after it had been frozen for 20 days. The iris was dark brown. The bill, except for the egg teeth, was entirely jet black. The posterior half of each tarsus was black; the anterior half was pinkish white for the distal two-thirds, then blending into a dark purplish pink base. The toes were jet black below and pinkish white above, with shiny black nails. Dorsally (above) the basal third of the webs was pale pinkish gray and the remainder dark gray tinged with maroon. Ventrally the webs were blackish tinged with dark maroon. This seemingly reversed coloration—pale above and dark below—may represent countershading that operates when the feet are extended posteriorly (R. W. Storer, in litt.).

The Marbled Murrelet chick was compared directly with the only known chick of the Kittlitz's Murrelet (*B. brevirostris*; University of Kansas 60504), which is said to be 1–2 days old (Thompson et al. 1966). The colors of the bill and eye are identical, and those of the tarsi, toes, and webs are similar. Each chick has 2 egg teeth, a pale belly, a buffy back marked with black, and a buffy head discretely blotched with blackish. In the Kittlitz's chick, however, the ground color of the head is paler and brighter—buffy yellow instead of Ochraceous-Buff; the abdomen is creamy white faintly tinged with grayish, instead of buffy gray; the breast is an unmarked, moderately dark gray, rather than concolor with the abdomen; and the upperparts posterior to the neck, rather than being Ochraceous-Buff strongly variegated throughout with blackish, are medium gray, lightly and evenly suffused (grizzled) with pale buffy yellow and broken only by two black spots on the midline of the middle and lower back. Each chick possesses a large black spot on the nape. A younger Marbled chick is needed to determine whether or not other spots on the head, neck, and back of the two species are homologous. The Kittlitz's nestling has a very dense patch of down on each side of the lower abdomen, merging in a crease along the midline; this down may function as extra insulation from cold ground. The age differential would not seem to account for the apparent absence of these patches in the Marbled Murrelet chick.

DISCUSSION

Relationships.—A number of authors, including Bent (1919), Peters (1934), and most recently Mayr and Short (1970), have merged *Endomychura* (*hypoleuca hypoleuca, h. scrippsi*, and *craveri*), with *Brachyramphus* (*marmoratus* and *brevirostris*) while retaining *Synthliboramphus* (*antiquus* and *wumizusume*). Storer (1945b), on the other hand, presented abundant evidence that *Endomychura* is closer to *Synthliboramphus* and that *Brachyramphus* is the most widely divergent of the 3 genera and deserves to be placed in a group by itself; pending further study, he preferred to maintain the separation of *Endomychura* from *Synthliboramphus*.

Our study of the downy plumages and nesting habits of the murrelets, based on data not available in 1945, strongly supports Storer's arrangement. Comparison of all 6 species of murrelets, including both races of *E. hypoleuca* (CAS; Museum of Vertebrate Zoology, Berkeley; University of Michigan Museum of Zoology), demonstrates that in the plumage color and pattern of the downy young, *Endomychura* and *Synthliboramphus* are much more similar to each other than either is to *Brachyramphus*. Chicks of the 5 forms included within the first 2 genera are essentially dark above and white below (see photograph of *E. h. scrippsi* in Bent 1919). They share the following characteristics: forehead and crown uniform black or dark gray; rump black; orbital region with a small white spot above and another below eye; chin with some black adjacent to lower mandible; throat, breast, abdomen, and posteriormost flanks essentially white; wing below mixed with gray and white; wing above solid dark gray or blackish on manus and anterior part of antebrachium; and thighs bicolored.

In *S. antiquus*, *S. wumizusume*, and *E. h. hypoleuca*, the entire back and, to a somewhat lesser extent, the sides, anterior part of the flanks, and dorsoposterior portion of the antebrachium are strongly grizzled. This grizzled effect results from an elongated grayish-white subterminal band on each otherwise black barb. In *E. h. scrippsi* and *E. craveri*, on the middle and lower back and the sides of the upper back, the subterminal bands are missing on some barbs and reduced in length on the remainder, thus producing a faintly spotted effect; elsewhere the spotting is very scattered and difficult to discern in the former and obsolete in the latter. A second important feature shared by *S. antiquus* and *E. h. hypoleuca*, but significantly not by *S. wumizusume*, is a large white auricular patch. This region in *E. h. scrippsi*, *E. craveri*, and *S. wumizusume* is blackish. The lores and temporal regions of *E. h. hypoleuca* are uniquely white, except for a small blackish crescent anteroventral to the eye. *E. craveri* has a blackish wedge extending from the side onto the breast.

Certain other plumage characters of the chicks exhibit degrees of variation that might prove useful in assessing relationships within this 5-form group were series to be studied: the extent and uniformity of the dark rump and pale flank patches; the darkness and hue of the sides, anterior flanks, and upperparts, especially the crown; the exact degree of grizzling or spotting; the amount and extent of the faint streaking resulting from the black hairlike tips on the otherwise white feathers of the underparts; the distribution of the dark feathers on the chin, which appear to be connected to the subocular region only in *E. craveri* and *S. wumizusume*; and the size of the white orbital spots.

Thus *Synthliboramphus* and *Endomychura* are linked by the numerous characters shared by all 5 forms; by the probable homology of the spotting in *E. h. scrippsi* and *E. craveri* to the grizzling in *S. antiquus*, *S. wumizusume*, and *E. h. hypoleuca*; by the similarity of *E. h. hypoleuca* to both *Synthliboramphus* species in the possession of strong grizzling and to *S. antiquus* in the presence of a white auricular patch; and by the resemblance of *S. wumizusume* to *E. h. scrippsi* and *E. craveri* in the possession of dark auriculars.

The chicks of the 2 *Brachyramphus* species, on the other hand, are unique among murrelets in possessing buff color on the back, rump, and head (including chin and throat); a strong pattern of blackish variegations or discrete spots on the back and head; and color on the breast and abdomen. The similarities between the chicks of the Marbled and Kittlitz's murrelets demonstrate their close relationship, whereas the relatively minor differences we interpret as cryptic adaptations to their respective nest sites.

Brachyramphus nests in the open, *B. marmoratus* on moss- or lichen-coated tree limbs, and *B. brevirostris* on the ground amid lichen-covered rocks (Thompson et al. 1966). The other genera nest in more or less enclosed situations, *Synthliboramphus* in burrows and *Endomychura* under low plants or in natural or slightly improved rock crevices (Bent 1919). In addition, the young of the 4 species of *Endomychura* and *Synthliboramphus* are precocial, while those of *Brachyramphus* are semi-precocial (Sealy 1973).

Cryptic coloration.—The Big Basin discovery enables us to construct a theory correlating the nesting habitat of the species with the widely divergent colorations of the egg, downy young, and breeding adult. Winter rains wash away the droppings from any previous nesting, quickly freshen the underlying, already green moss, and cause the moss in the brown area surrounding the ring to send up new shoots. Thus the green egg blends as soon as it is laid. The spots on the egg could be disruptive in nature or could mimic shadows or the fruiting capsules of moss.

The dark brown plumage of the breeding adult matches almost perfectly

the predominant color of moist Douglas-fir bark; and the rufous scapulars simulate the small, rusty bark streaks. Although the plumage could simulate a bare or freshly broken portion of limb (Sealy 1974), we believe that the positioning of the nest near the mossless south side of the trunk is significant both in allowing the incubating bird to blend with bark and in reducing silhouetting against day and night sky.

The color of the pale down on the head and upperparts of the nestling closely matches the weathered portions of the droppings and the surrounding brown moss: the dark down probably simulates shadows. We speculate that the moss surrounding the ring of droppings changes to brown from an interaction between sunlight (or some other weathering agent) and leachings from the ring; apparently neither acts alone, as the moss both beneath the droppings and exposed to sunlight on the rest of the limb remains green. Possibly the phenomenon is similar to that known to horticulturists as "fertilizer burn" (D. E. Breedlove, pers. comm.). We do not believe that the brown moss owes its color to salt water introduced by the adults, since we found no salt crystals, nor to some substance from the mouths of the adults, because the sitting birds almost certainly would align themselves with the long axis of the bowl (NNE-SSW), whereas the brown encircles the nest.

We suspect that the adults, rather than the chick, initiate the ring of droppings, because the brown color of the droppings and surrounding moss would seem to be of greatest selective value to the chick if present at the time of hatching. The droppings of the chick increase the dimensions of the ring and probably the brown area. The conspicuousness of the raised white ring of droppings is reduced by the buffy coloration of its uppermost layers. Probably the ring has no meaning to predators and may be advantageous in obscuring the outline of the nestling and perhaps even in providing a target for adults approaching in darkness.

Siberian nest.—A nest of *B. m. perdix* was found on 17 June 1961 by Kuzyakin (1963) about 12 km northwest of the city of Okhotsk, Siberia. The nest tree was a larch (*Larix dahurica*), 12 m tall and 17 cm in diameter (at 1.5 m), located 6–7 km from the sea at the edge of a forest. The nest, containing one egg, was situated 6.8 m from the ground and 25 cm from the trunk on a cushion of dendroid lichen (*Bryopogon* sp.) that grew on a branch with a wide flat surface formed by a dense intertwining of small twigs. The nest cushion measured 14 × 17 cm in diameter and 3–4 cm in height, and the hollow (bowl) 6 × 9 cm diameter and 2–2.5 cm deep.

The Big Basin and Siberian nests share several important characteristics: both were located near the trunk on a horizontal branch thickly covered

with vegetation; had similar dimensions; were little more than a depression in the natural vegetative growth on the limb; and, although placed at different heights, afforded easy access to the ocean, which was about the same distance away. Two other similarities are doubtfully significant: both nest trees were near streams and bore branches below the nest limb.

Nest site.—Tree nesting (Harris 1971, Savile 1972, et al.) is now proven. That the Marbled Murrelet sometimes nests in burrows, rock crevices, and river gravels, as suggested by some authors (e.g. Darcus 1927, Gabrielson and Lincoln 1959, Guiguet 1971; but see also Sealy 1974), seems highly unlikely in view of the positions of the Siberian and Big Basin nests and the strong adaptations to tree nesting exhibited by adult, egg, and chick coloration. However, we cannot as yet rule out these other possibilities, for the nesting behavior of the species may differ from one locality to another, especially where large trees are unavailable, such as on Mittelnach Island, B. C., near which Sutton and Semple (1941) collected an egg from the oviduct of an adult.

We suspect that the Big Basin nest site was used traditionally. No apparent peculiarity of the bowl would prevent the natural growth of moss that would occur if the nest were unattended over a period of years. Therefore the adults probably removed the moss. That every vestige, including the rhizoids, could or would have been pecked or scratched away in a single season by the adults (and subsequent movements of the chick), seems to us highly unlikely. Rather, we suspect that the moss was removed and prevented from regrowth, probably inadvertently, over a period of years. The quantity of droppings in the Big Basin nest is not helpful; a single year's use could account for the amount, and the abundant rainfall in Big Basin probably would dissolve away accumulations from previous years. The few old eggshell fragments that might become entrapped in the moss probably could not be told from others originating from the same adult.

To aid future workers, we here summarize those characteristics of the Big Basin site that may prove significant in nest location, at least in the southern portions of the range of this subspecies. The nest was found in a (1) humid (2) virgin forest that was (3) near coastal feeding areas, (4) contained water-filled streams, and was in part composed of (5) a large species of tree (Douglas-fir) with (6) an open crown structure and (7) bark colored like the plumage of breeding adults. The nest was positioned (8) high above the ground, at a point allowing (9) easy access to the exterior of the forest, and (10) next to the trunk on a (11) wide, (12) horizontal, (13) southward-projecting limb that was (14) densely covered with (15) green moss and (16) protected by a slanting trunk and a closely

overhanging branch. We feel that the most critical factors are the following: the ease of access (which may dictate the height of the nest and nest tree and require a tree species with an open crown structure); the slope, diameter, and vegetative coating of the nest limb (the last two depend on, respectively, the age and humidity of the forest); and the color and proximity of the trunk. The distance to coastal feeding areas probably is determined by the availability of suitable nesting forests, with preference shown for the closest forests. The southward direction of limb projection could be significant in providing solar heat for the chick, proper wind conditions for landing and takeoff of adults (and young?), and a mossless trunk side.

The summer range of *B. m. marmoratus* corresponds closely with the distribution of the coastal portions of the moist coniferous forest biome (Shelford 1963). In Alaska this biome terminates on Kodiak Island and the adjacent mainland, which are also the northwesternmost points where the murrelet summers commonly. Murrelet records from farther north and west in Alaska for which dates are given by Gabrielson and Lincoln (1959), except for summer occurrences at Unalaska, extend from early fall into winter and hence represent nonbreeding birds.

The following 13 species of trees are extensively and coastally distributed within this biome and have branches wide enough to support a nest: Pacific silver fir (*Abies amabilis*), noble fir (*A. procera*), giant fir (*A. grandis*), western white pine (*Pinus monticola*), Sitka spruce (*Picea sitchensis*), western hemlock (*Tsuga heterophylla*), Douglas-fir, coast redwood, giant-cedar (*Thuja plicata*), California-laurel (*Umbellularia californica*), red alder (*Alnus rubra*), black cottonwood (*Populus trichocarpa*), and big-leaf maple (*Acer macrophyllum*). The 9 conifers are tall and open enough to provide easy access for adult murrelets. The 4 angiosperms, however, probably may be eliminated as potential nest trees by virtue of the limited access afforded by their rather closed crowns and smaller stature, the latter characteristic usually resulting in enclosure by the taller conifers. The angiosperms, as well as certain of the conifers, may well possess other undesirable characteristics, such as sloping branches, improperly colored or textured bark, or insufficient epiphytic growth (see below). Although tree species that attain large size and hence wide branches probably provide the best sites, the small stature of the Siberian nest tree indicates that we cannot entirely eliminate smaller trees in which conditions such as unusual twig growth produce suitable platforms.

None of the 13 trees is found throughout the summer range of *B. m. marmoratus*. The Douglas-fir, for example, ranges only from central California to northwestern British Columbia. Thus the birds must use at least

2 species of trees. As noted previously, the Siberian nest was in an Old World species of larch (*Larix dahurica*). Harris (1971) reports a young bird taken from beneath "a cedar, probably the western red cedar (*Thuja plicata*)," felled on Vancouver Island. Guiguet (1956) mentions an adult and broken egg found under a "large hemlock" (presumably *Tsuga heterophylla*) logged on the Queen Charlotte Islands. In California south of the mouth of San Francisco Bay, the only large conifers are the coast redwood and Douglas-fir. We suspect that in this region the murrelets would usually select Douglas-firs instead of coast redwoods because the latter, even though larger and twice as abundant at the Big Basin site, do not support a sufficiently dense growth of moss or lichen (D. Breedlove, pers. comm.; pers. obs.).

Number of broods.—The temporary persistence of a pale ring of droppings and surrounding brown moss after a chick has fledged may preclude the use of a nest for a second brood during the same nesting season. A new egg would not blend in until most of the droppings were washed away to expose the underlying green moss. Also, the fouling of the feathers that might result from an adult incubating atop the messy droppings of its previous chick would seem highly disadvantageous to an aquatic species.

Clutch size.—Our findings support Sealy's (1974) determination that clutch size in the Marbled Murrelet is one. In addition to the presence of a single chick in the Big Basin nest, evidence is provided by the nest bowl, the effective size of which is too small to accommodate 2 eggs measuring 58.5 × 39.5 mm each (Sutton and Semple 1941).

Fledging.—Available evidence suggests that young Marbled Murrelets breeding in forests reach the ocean by flying directly from the nest sites or nearby trees, rather than by walking or swimming as suggested by Kuzyakin (1963). The stream near the Siberian nest was reduced to a series of disconnected pools and thus could not have provided a convenient avenue to the sea. In August 1974 the Big Basin stream beds contained no more than a trickle of water, probably not enough to float a murrelet, and were clogged with debris that a chick could negotiate only with great difficulty. Accidents could account for the few known groundings. If terrestrial or stream travel were the rule, many more young should have been discovered, especially in such well-populated localities as Prairie Creek Redwoods State Park, Humboldt Co., California (Baldridge et al. 1970) and Big Basin. Mammalian predators surely exert strong selective pressures against ground travel, especially considering that a young bird probably is unable to take flight from the ground in a windless forest (Storer 1945a) and would have to walk many kilometers from its nest to the ocean.

SUMMARY

The first nest of *Brachyramphus m. marmoratus* was found on 7 August 1974 in Big Basin Redwoods State Park, Santa Cruz Co., California. The nest, located 45 m above the ground at the base of a limb of a Douglas-fir, consisted of a depression in bark nearly surrounded by murrelet droppings atop living moss. Eggshell fragments removed from the nest are similar in color to previously described eggs but exhibit one new spot color. A downy nestling, the first of the species known to science, is described and compared to *B. brevirostris*; morphological similarities demonstrate their close relationship, while differences are believed to be cryptic adaptations to nest site. The nesting habits and downy plumages of these 2 species support the treatment of *Brachyramphus* as a genus distinct from *Endomychura* and *Synthliboramphus*. A theory is presented that correlates the nest site with the cryptic colorations of the breeding adult, egg, and chick. The nest site is similar to that of *B. m. perdix*, proves tree nesting, and is thought to be used traditionally but not more than once per year. The characteristics of the Big Basin site are summarized to facilitate the future discovery of nests. The summer range of the murrelet corresponds closely with the distribution of the coastal portions of the moist coniferous forest biome. Within this area optimal nesting sites are provided by about 9 species of trees, all conifers, of which the birds must use at least 2. In central California possibly only the Douglas-fir is used. Evidence indicates a clutch size of one. The fledglings are believed to reach the ocean by flying.

ACKNOWLEDGMENTS

On behalf of the ornithological community, we express our deep gratitude to Hoyt Foster, of the Davey Tree Company, whose keen awareness led to the original discovery and whose subsequent labors provided the specimens and many valuable notes. We are grateful to C. Jones and California State Park Rangers D. Verardo and D. Friend for retrieval and care of the nest and chick; D. Toren for identification of the moss; D. E. Breedlove and E. McClintock of the California Academy of Sciences for aid in botanical matters; M. Frinke for measurements of the nest tree; N. K. Johnson of the Museum of Vertebrate Zoology, University of California, Berkeley, and R. M. Mengel of the Museum of Natural History, University of Kansas, for use of specimens in their care; S. A. Mitchell for the habitat photograph; and A. Baldridge, I. McT. Cowan, R. Gill, J. Lewis, D. A. Manuwal, H. Thiers, M. D. F. Udvardy, and M. Watson for useful data. We thank S. G. Sealy and R. W. Storer for their thorough examination of the manuscript and the latter for loan of a specimen.

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California Academy of Sciences, Golden Gate Park, San Francisco 94118; 485 Manzanita, Felton, CA. 95018; and 9442 Hayes Street, Apt. B, Riverside, CA. 92503. Accepted 20 May 1975.

ASPECTS OF THE BIOLOGY OF THE CHESTNUT-SIDED SHRIKE-VIREO

Jon C. Barlow and Ross D. James

The Chestnut-sided Shrike-vireo (*Vireolanius melitophrys*) occurs above 1850 m in upper tropical and subtropical zones from the Mexican states of Jalisco, San Luis Potosi, and Vera Cruz (Blake 1968) south to the volcanic highlands of western Guatemala (Land 1970). Little is known of this species in the field and only a few reports concerning aspects of its general biology have been published (Davis 1962, Schaldach 1963, and Rowley 1966).

The Chestnut-sided, with the Emerald (*Vl. pulchellus*) (*Vl.* will be used hereafter to indicate *Vireolanius*) and Slaty-capped (*Vl. leucotis*) shrike-vireos, both of humid lowland tropical forests, comprise the subfamily Vireolaniinae, and with peppershrikes (Cyclarhinae) and vireos (Vireoninae) constitute the family Vireonidae (Blake 1968). Our study describes the first known nests, vocalizations, and aspects of the breeding behavior and ecology of the Chestnut-sided Shrike-vireo and compares these with similar data for other vireonids.

MATERIALS AND METHODS

Plumage characters and size.—The boldly patterned Chestnut-sided, the shimmering green Emerald, and the bright yellow and green Slaty-capped shrike-vireos contrast sharply with other vireonids which are mainly species of plain or subdued plumage. *Vireolanius melitophrys* and the Black-capped Vireo (*Vireo atricapillus*) are the only vireos that demonstrate sufficient dimorphism in adult plumage characters to allow ready identification of the sexes in the field. In this shrike-vireo females are paler than males, especially ventrally, and have a narrower bar of chestnut across the breast and smaller areas of this shade on the sides of the breast and flanks than do males.

No sex-related differences in size are apparent in the Chestnut-sided Shrike-vireo. Adults are about 17.5 cm in total length, and weigh about 33 g. Among vireonids only the Cozumel Island race of the Rufous-browed Peppershrike (*Cyclarhis gujanensis insularis*) equals the Chestnut-sided Shrike-vireo in size.

Study area and habitat.—Beginning in November 1971 fieldwork was undertaken at 2 locations, 10 km apart, at about 2880 m in the mountains of northern Morelos in mixed coniferous-deciduous forest where the Chestnut-sided Shrike-vireo was known to occur. The sites resembled each other in composition of vegetation but differed in the degree of exploitation by local people. About 3 km W of the village of Huitzilac the forest covering the southeastern slopes of the higher peaks was essentially continuous although cutting trees for charcoal was widespread. In contrast, at the second locality 5 km S of Tres Cumbres along route 95 to Cuernavaca, some large trees and most of the undergrowth had been cleared for farming, or by woodcutters.

FIG. 1. Disturbed pine-oak forest S of Tres Cumbres, Morelos (2880 m), in a Chestnut-sided Shrike-vireo territory.

resulting in a mosaic of small fields and patches of forest (Fig. 1). We worked in both localities for parts of 3 days in November 1971 and 6 days in November 1972 and 16 days each in May 1972 and 1973.

Where relatively undisturbed, the mixed forest of the study areas comprised as well as pines (*Pinus* sp.), a variety of broad-leaf deciduous trees, which averaged about 12 m in height; a few large oaks (*Quercus* sp.) reached 20 m. The oaks, festooned with a variety of epiphytes, grew mostly along drainages and in narrow ravines coursing down the mountain slopes. Many of the pines were more than 30 m tall. Underbrush consisted of fairly dense leafy shrubs and tangles of vines. In vegetation, our study areas were consistent with descriptions from other parts of the range of the Chestnut-sided Shrike-vireo of pine-oak habitat, ranging from open scrub (Davis 1962) to tall, dense, humid or cloud forest with fairly complex canopy (Schaldach 1963, Rowley 1966). In May heavy rainfall could be expected daily in the area. In November tree-level cloud cover occurred occasionally but rain was sporadic.

Field and laboratory procedures.—Activities at the nests were observed with binoculars from concealment so as to minimize disturbance. We followed pairs or individuals in the study sites. Distances among farthest song perches were used for rough approximations of territory size. We studied foraging behavior of shrike-vireos by noting type of prey and the position and kind of sites from which food was taken.

Vocalizations of 6 males and 2 female Chestnut-sided Shrike-vireos were taped in May of 1972 and 1973 with a Uher 4000 Report-L tape recorder using an M537 Uher microphone mounted in a 44.5 cm Gibson sound parabola. Sound spectrograms were produced with a 6061B Kay Electric Sona-Graph using the wide band setting.

RESULTS AND DISCUSSION

Status.—Previous authors have not considered Chestnut-sided Shrike-vireos to be common (Miller et al. 1957, Edwards 1972). However, we found this species to be locally common in our study areas. In the first visit to the 2 sites in November 1971 the only shrike-vireo encountered was a female south of Tres Cumbres. At that time we knew nothing of the vocalizations of the species and thus were relying solely on sightings. On 6 May 1972 near Huitzilac, vocalizations of both members of a pair were recorded. In the next few days within 1 km of the place where the first pair was encountered we saw 10 additional birds and heard as many as 15 calling. In November of 1972 we observed at least 5 males and 1 female in the 2 circumscribed study sites. In May 1973 we did not search extensively for birds near Huitzilac but rather concentrated on a pair whose nesting habits we studied. In the same year, near Tres Cumbres we found 3 pairs in an area about 600 m in diameter.

Vocalizations.—Males sang at irregular intervals throughout the day in May but only occasionally and for short periods in November. In the breeding season the highest sustained rate of song was noted in conjunction with the early stages of nest-building. For example on 12 May 1973 the male associated with one of the nests sang 15 to 30 songs in bouts approximately 1 min in length at 10 min intervals from 09:00 until 11:30. As in most oscines, song largely ceased in early afternoon and was followed late in the day by a second short period of accelerated singing. Many kinds of vireos tend to sing more than other passerines in the same habitat (Barlow 1962). The Chestnut-sided Shrike-vireo, however, seems less vociferous than any of the other 35 vireonid taxa with whose singing patterns we are familiar.

Singing postures.—In the most frequently observed singing posture the body of the male shrike-vireo was maintained at an angle of about 50° from the horizontal. Occasionally in times of agitation the body angle approached 80°. The bill was held at right angles to the body and the head was not visibly bobbed or otherwise moved. The wings and tail were not moved appreciably. Song in flight was only noted when combatant males sang the primary song while flying short distances and in supplanting attacks.

Types of vocalizations.—Six vocalizations were readily distinguishable in the field which were later confirmed with spectrographic analysis. The sounds are divisible into songs and calls.

(1) Primary song (Fig. 2A). The monosyllabic primary song, given only by the male, begins as a short, ascending, whining moan which becomes a descending, wailing whistle terminating abruptly. The song may

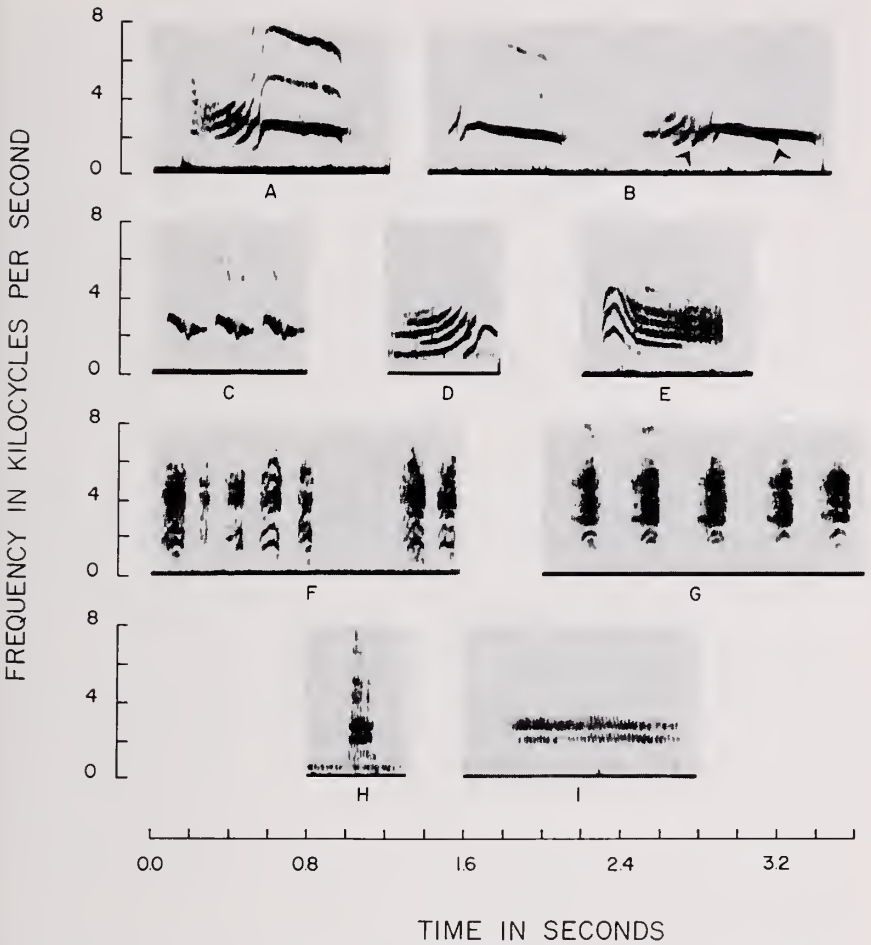

Fig. 2. Shrike-vireo vocalizations. A. Primary Song; B. Fight ♂♂ *Vl. melitophrys*; C. Primary Song of *Vl. pulchellus*; D. Short Song; E. *Myaaaah* Call; F. Distress Call; G. Distress Call; H. Contact Call; I. Buzz-rattle.

be given singly or repetitively and the interval between successive songs ranges from 0.4 sec, in a male responding either to playback of taped song or to an intruding male, to 1.2 sec in an unstressed male simply singing from some perch within his territory. There is probably a little individual variation in song length among males as 10 songs each of 3 different males averaged in length 0.74 sec, 0.72 sec, and 0.93 sec respectively.

In the short ascending part of the song, energy is concentrated in the first 3 of 4 harmonics whereas energy in the whistled portion is concen-

trated in the fundamental. In some tracings second and third harmonics are seen at about 2 KHz intervals above the fundamental, but these may be electronically enhanced artifacts. Pitch of songs of the above 3 birds averages between a low of 1.25 KHz and a high of 4.08 KHz (range 1 to 4.5 KHz).

In this species song appears to function in sex and species recognition and to stimulate the female in nest-building and courtship. In the latter context, the male accompanies the female with song as they gather nesting material or forage and as they approach the nest. Primary song was clearly audible at distances of 400 m. Since the song does not attenuate rapidly we suggest that it provides special locative advantages should the sexes become widely separated in an environment where prevalent foggy conditions, dense vegetation, and mountainous terrain may greatly reduce visibility.

On 5 May near Huitzilac, high intensity primary song was heard as we observed 2 males fighting, chasing, and directing supplanting attacks at each other. Throughout these activities both birds sang rapidly, sometimes almost antiphonally. Since their individual songs varied in the degree of overlap or did not overlap at all (Fig. 2B), high intensity countersinging rather than antiphony was probably involved.

The primary songs of the Chestnut-sided Shrike-vireo and the closely related Emerald Shrike-vireo (Fig. 2C) bear no resemblance to one another other than that they both may involve the repetition of a single sound; however, repetition of the same syllable or song is characteristic of the vocal patterns of many vireonids. The song of the latter species which sounds very much like that of the Tufted Titmouse (*Parus bicolor*) comprises a single syllable uttered 3 times in rapid succession. However, greater disparities in songs are found among species in the genus *Vireo* (e.g. the monosyllabic trill of the Blue Mountain Vireo, *V. osburni*, in contrast to the complex song of the Thick-billed Vireo, *V. crassirostris*) and without quantitative study such differences should not be given undue taxonomic importance.

(2) Short song (Fig. 2D). This non-musical vocalization is structurally derived from the primary song. The descending fundamental is short (0.2 sec in length), terminating as an abrupt "whap". This song, given singly, was uttered by the male at the first nest discovered on 3 occasions when he approached or worked on the nest alone. Since the female twice arrived at the nest shortly after the male sang in this manner, we have assumed that the song served as a signal to her.

(3) *Myaaaah* call (Fig. 2E). Sonagrams show that there are some structural resemblances between this call and the initial part of the pre-

vious song. However, the *myaaaah* sound is widespread among vireos of the subgenus *Vireosylva* as an aggressive and locative call (pers. observ.). The female, paired with the male first encountered on 5 May 1972 near Huitzilac, was the only bird that was heard to give this call. Five of these calls were uttered at 2.7 sec intervals as both she and the male flew rapidly from perch to perch in response to playback of the song of this male. In this context the call apparently had an aggressive function serving to threaten an intruder.

(4) Distress call (Fig. 2F, G). Hand held birds gave typical passerine distress calls (see Stefanski and Falls 1973) comprised of syllables of the same or different length as shown. Intervals between syllables varied as a function of the degree of agitation of a bird. Although louder and more harsh, distress calls of this species resembled those of other vireos with which we are familiar.

(5) Contact call (Fig. 2H). Single low-pitched buzzy calls were uttered by both sexes at the nest as they worked together or alone or as the female departed. This call differs structurally from distress calls.

(6) Buzz-rattle (Fig. 2I). This harsh call structurally resembles contact notes but is appreciably longer. It was uttered by both sexes. When approaching the nest in the absence of the female, the male sometimes sang briefly or gave this call. Several times then the female appeared as the male departed. Similarly, the female uttered the buzz-rattle once when she came into the nest alone. The male appeared within a few seconds. This call may have served as a signal between the sexes indicating to the absent (but presumably nearby) partner the presence of the other adult at the nest.

Territorial behavior.—Territorial behavior, as observed in May 1972 and 1973, did not differ appreciably from that of the 20 species of vireonids with which we are familiar in this context. In the breeding season pairs of Chestnut-sided Shrike-vireos maintain mutually exclusive territories perhaps as large as 4.2 ha. The one territory near Tres Cumbres which we regularly visited in May 1973 was located on a west facing slope of about 35° and encompassed about 4.1 ha of open pine forest, with scattered large oaks, open fields, and brushy ravines. On the east this territory was bounded by a 4-lane limited access highway, which the birds were not seen to cross, and on the north, south, and west by territories of other pairs of shrike-vireos. Old highway 95, which paralleled the 4-lane highway, passed from north to south through the territory, bearing fairly heavy automobile and diesel truck traffic which did not seem to disturb the birds. This pair regularly ranged as far as 300 m from the nest-tree.

Adjacent males demonstrated countersinging and gave agitation calls at the times when mutual boundaries were approached. On 6 May 1972 two vocal males and a third silent bird chased each other. One individual directed supplanting attacks at the second male as both sang loudly. These birds fought intermittently for several minutes at one point clutching at each other's feet and uttering distress calls while beating each other with their wings. The entire encounter lasted 3 min after which one male, still singing, accompanied by the silent bird moved down the slope and the other male, also in full song, flew up the mountainside; both could be heard for another 10 min.

Response to playback of taped song in spring consisted of vigorous singing and low rapid flights from perches in nearby trees, over and around the speaker. Song was not accompanied by wing flicking as seen in Bell's Vireo (*Vireo bellii*) (Barlow 1962); however, one male fanned his tail during playback and erection of crown feathers occurred frequently in this context.

One pair of birds and a single male responded to taped song on both 3 and 6 November 1972, near Huitzilac at the same places on each of these dates. Each male approached the recorder but made only 1 or 2 flights over it before landing in a nearby tree to sing. Therefore we think that the birds may stay in the vicinity of their breeding territories outside of the breeding season. Lowery and Newman (1951) also reported birds in Vera Cruz at the same localities in May and December.

We saw no interactions of consequence between shrike-vireos and any other species of birds in the breeding season. Once near Huitzilac we observed a Warbling Vireo (*Vireo gilvus*) foraging within 3 m of a nest as a female Chestnut-sided Shrike-vireo was building, but neither species seemingly took note of the other. Hutton Vireos (*Vireo huttoni*) sang regularly near both the shrike-vireo nests studied but we never noted shrike-vireos responding to the vireos. Noisy flocks and family groups of Gray-barred Wrens (*Campylorhynchus megalopterus*) moved regularly through shrike-vireo territories without incident. These 2 species often foraged within a meter of one another in the same tree. Twice in late autumn we saw female shrike-vireos associated with foraging flocks of much smaller species including Ruby-crowned Kinglets (*Regulus calendula*), Yellow-eyed Juncos (*Junco phaeonotus*), Mexican Chickadees (*Parus sclateri*), Plumbeous Solitary Vireos (*Vireo solitarius plumbeus*), Cassin's Solitary Vireos (*Vireo s. cassini*), and Brown Creepers (*Certhia familiaris*).

Foraging.—Vireonids forage on arthropods by gleaning from foliage, by hawking from perches, and by stalking on twigs, larger branches, and even the trunks of trees. Thin billed forms such as the Red-eyed Vireo (*Vireo*

olivaceus) mostly glean whereas heavier billed species as the Yellow-throated Vireo (*V. flavifrons*) favor bark of larger branches (James 1968).

The Chestnut-sided Shrike-vireo has a massive bill but surprisingly takes most prey from leaves and less frequently from bark. Pine needles, epiphytes, and filamentous lichen are probed and broad leaves are inspected closely. Inner foliage is favored over outer canopy. A foraging bird searches from a perch then hops or flies to another, a meter or so distant. Occasionally an individual hangs beneath a leaf cluster then flutters to a site 1 or 2 m below. Rarely birds hover at clusters probing or plucking insects from them. One 3 min foraging session on 14 May 1973 comprised 25 individual bouts, 23 involved upright gleaning of foliage from perches; one involved hanging beneath a leaf cluster; and one hovering at a cluster. We observed birds foraging from .6 m to 30 m (mode = 8 m) above the ground.

In the breeding season the male and the female typically foraged from .3 m to 4 m apart and the female was usually the first to leave a tree or shrub. The male would follow within a few seconds. Males often sang while foraging but feeding was interrupted by nest-building, preening, and periods of inactivity. Peaks of foraging occurred in the morning between 06:30 and 08:00 and in the afternoon about 16:30.

Although primarily insectivorous, *Vl. melitophrys* apparently also eats some plant material. Davis (1962) mentioned insect fragments including beetle parts and the head of an ant in 2 stomachs. Schaldach (1963) found small spiders and elytra of beetles of the families Curculionidae and Brentidae in crops which he inspected. Schaldach also thought that in the dry season in Colima, that shrike-vireos were eating seeds and hawthorne (*Crataegus*) "apples". Food items we observed being eaten comprised caterpillars, wasps, grasshoppers, true bugs, beetles, and some plant material. Large caterpillars, perhaps 70 mm in length, were not swallowed directly but were held in the bill and either shaken or beaten against a branch. Large, hard-bodied prey were held in one foot and picked apart with the beak, whereas smaller items were swallowed whole.

Nest-building.—The nidification of *Vl. melitophrys* has not been described. Rowley (1966) predicted that the nest, when found, would be well concealed among epiphytes. This did not prove to be true. On 5 May 1972 near Huitzilac, behavior of the first pair of birds suggested that construction of a nest might be underway. We were unable to make further search that year. On the morning of 7 May 1973, near Huitzilac at the exact site of our 1972 encounter, we found a pair nest-building. The female made several flights of at least 100 m with strands of grass in her beak, terminating each time in the same grove of Mexican oak (*Quercus mexi-*

Table 1

Time (in seconds) and Frequency of Active Nest-building by Chestnut-sided Shrike-vireos Observed in 1973

	Nest 1			Nest 2								
	8 May (09:00–16:00)			11 May (08:30–17:00)*			12 May (09:00–14:30)**			14 May (07:40–14:30)		
	N	mean	range	N	mean	range	N	mean	range	N	mean	range
♂ alone building	2	42.5	(42–43)	2	75	(60–80)	2	90	(60–120)	4	150	(30–270)
♂ alone not building	3	42.5	(25–60)				1	NR***				
♀ alone building	6	120	(30–300)							2	45	(30–60)
♀ alone not building	3	60	(10–110)	1	10		1	NR				
♂, ♀ at nest	3						1					
♂ building	(2)	45 each					(1)	240				
♂ not building	(1)	NR										
♀ building	(3)	105	(60–150)									
♀ not building							(1)	NR				
Totals	17			3			5			6		

* All visits between 09:26 and 09:33.
** All visits between 11:00 and 12:13.
*** NR = not recorded.

canus) and sweet leaf (*Symplocos* sp.). At 09:00 on 8 May 1973, James found a nest (Nest 1) in this grove, in a sweet leaf 10 m tall and 15 cm in diameter at the base. The nest, which was not well concealed, was of typical vireo pensile construction, and was suspended from a subterminal fork of a small branch on the west side of the tree 1.5 m from the trunk and 8 m above the ground.

On 10 May south of Tres Cumbres we began following a pair of foraging birds at 08:00. At 13:00 we had moved from an area 200 m west of old highway 95 to a grove of large pines east of this road when we observed both birds tugging at filamentous lichen in a large pine about 25 m above the ground. The male flew 30 m farther up a slope into a 10 m Mexican oak. The female was briefly lost from sight. Moments later we sighted both birds at work on a nest (Nest 2) which was just beginning to take on a recognizable pensile shape. This nest, on the west side of the tree, was suspended 7 m above the ground from a subterminal

fork about 30 cm from the tip of a lateral branch 2 m in length. The activities of local people near Huitzilac made continuous daily observations of Nest 1 difficult so that our attention was largely focused on Nest 2. Table 1 summarizes observations of active nest-building at Nests 1 and 2.

Both sexes took part in building Nest 1 which, when first seen, was a recognizable bag but was so loosely woven that it could be seen through. Work on the nest involved emplacement of plant or animal material and/or weaving and molding of the structure. The pattern of building activity comprised 2 or 3 bouts from 1 to 3 min apart followed by absences from the nest varying between 16 and 104 min. We visited this nest site briefly thereafter on 12, 15, and 18 May, finding on 12 May that construction had progressed appreciably since the original discovery. On 18 May the nest was essentially complete and the female was beginning to sit in it for increasingly longer periods preparatory to laying. At this time we took the nest because charcoal makers were cutting all trees 10 m from the nest tree and were moving steadily closer.

At the time of its discovery, Nest 2 was in an earlier stage of bag construction than Nest 1. Both adults were active in building on 10 May. On 14 May prior to 11:00 no building occurred although we heard the male singing near the nest tree 7 different times. Heavy rain fell fairly regularly near Tres Cumbres between 10 and 14 May and it was cool and overcast for much of the rest of the time. The slower pace of building at Nest 2 may have been influenced somewhat by these conditions. On 17 May, after heavy rain in the early morning, the area was shrouded in fog and the birds made no visits to the nest between 10:00 and 13:35, although the male sang briefly near the nest tree once. On 18 May it again had rained early in the morning but by the time of our arrival at 12:35 it was sunny and warm. Between 12:35 and 16:00 no building occurred, although the male sang near the nest tree twice and the female was seen once tugging at lichen growing on a nearby pine. On 1 June Nest 2 was examined for us by Sr. M. Ramos O., who reported that the nest was completed, but contained no eggs and that the adults were not in evidence.

At Nest 1, which was in a more advanced stage of construction when found by us, the female did a greater portion of the building. At Nest 2, in an earlier stage when first seen, the contribution of the male exceeded that of the female. Although too small a sample upon which to base definitive conclusions, nonetheless there is an indication, confirmed in other vireonids (Barlow 1962, James 1973) in which both sexes participate in building, that the male predominates early in construction and is gradually replaced by the female as building continues.

FIG. 3. Nest 1—first known nest of *Vireolanius melitophrys* in a sweetleaf (*Symplocos* sp.).

Externally Nest 1 (Fig. 3) measured 100 mm in maximum diameter, 80 mm in minimum diameter, and was 66 mm deep from rim to bottom. Internally the nest measured 70 mm in maximum diameter, 60 mm in minimum diameter, and 50 mm deep. The branches of the fork from which the nest was suspended were 6 and 8 mm in diameter and the fork subtended an angle of 45°. The nest was lined with fine grasses, pine needles, and fibrous plant parts. The bag was largely constructed of filamentous lichen, woven together with spider webbing, and adorned on the exterior with spider egg cases. Except for being larger, the nest closely resembled nests of the 14 species of vireos with which we are familiar. Nest 1 was completed between 8 and 18 May. Judging from our experience with building rates in vireos and extrapolating accordingly, about 20 days were required for total construction. Progress at Nest 2 was slower and as much as 25 days may have been required for its completion. Certainly so large a nest as that built by the Chestnut-sided Shrike-vireo could not be finished very rapidly at the rate of no more than 5 or 6 building

trips per day. By comparison, nests of *Vireo bellii* were completed in 5 days in Kansas (Barlow 1962) and those of the Gray Vireo, *V. vicinior*, in 6 days in Texas (Barlow, pers. observ.).

Nesting material comprising plant fibers, lichen, and animal silk was gathered anywhere within the territories. Occasionally material was obtained in the nest tree but more typically the adults secured items between 20 m and 200 m from the nest site. At 08:00 on 8 May 1973, near Nest 1, we saw a female hanging upside down by one foot while extracting spider webbing with her bill from a bromeliad growing on the underside of a branch of a large oak. On several occasions we saw adults pulling on filamentous lichen and other plant material.

Behavior at the nest and courtship.—Nest-building and courtship activities are intimately intertwined in vireos (Barlow 1962). As mentioned previously, in the Chestnut-sided Shrike-vireo the male travels about the territory with the female, accompanying foraging and building activities with song. Although the female may come to the nest alone, the male is never far away. He usually sings as she arrives and often as she departs. The male usually punctuates his visits to the nest with song or other vocalizations. When members of a pair exchange places at a nest under construction, several contact notes may be uttered. Copulation was observed at Nest 1 on 18 May. At 10:00 the female was seen first in the nest and shortly thereafter on a branch 2 m above it. She gave several emphatic buzz-rattle calls. Then the male flew into the nest tree and the female crouched in a solicitory attitude with her body at right angles to the branch upon which she was perched. He mounted her for 3 sec without attendant physical displays or audible vocalizations. No displays followed copulation. The birds separated, sat quietly near each other for about 15 sec, and then flew off together.

Other aspects of the breeding season.—The initiation of reproductive behavior in the Chestnut-sided Shrike-vireo sometime between late April and early May roughly coincides with the beginning of spring rains. Our observations (5 to 20 May) in Morelos covered part of the period of nest-building. Although the timing of maximum gonadal development was not determined in our study, it doubtless coincides with the terminal stage of nest-building when copulation occurs as is the case in many vireonids (Barlow 1962). The earliest seasonal record available in this species is of a female with a brood patch and shelless egg in her oviduct from 19 km S Morelia (2440 m), Michoacán, taken on 28 April 1961 (Davis 1962). Possibly breeding activities in Michoacán are 2 to 3 weeks in advance of what we observed in Morelos. Miller et al. (1957) listed evidence of breeding in June at several Mexican localities. Rowley (1966)

reported another female with a well-defined brood patch and 3 ruptured follicles from La Cima (1960 m), Oaxaca, secured 16 June 1963. This record suggests a clutch size of 3 in this species. The only other insights available concerning reproductive biology are the capture of a bob-tailed fledgling attended by an adult on 7 July, 6.4 km N San Andres Chicahuaxtla, Oaxaca (Rowley 1966), and another young, a male (MMNH 22582) taken 16 August 1962, 1.3 km W La Jolla, Veracruz. Little else is known of the stages of the breeding cycle already discussed and nothing is known of egg-laying, incubation, or brooding.

Concluding remarks.—The Chestnut-sided Shrike-vireo resembles smaller vireos (Vireoninae) in territorial, courtship, and nesting behavior and in pattern of singing e.g. repetition of a particular syllable or syllables. Foraging strategy is also similar to that of smaller vireonids, reminding us most of that of Solitary Vireos (*V. s. plumbeus*) (pers. observ.). The nest of *Cyclarhis gujanensis* is of typical vireonid pensile construction (Skutch 1967). Thus vireos, greenlets (*Hylophilus*), peppershrikes, and shrike-vireos have the same type of nest, suggesting that these birds are closely related and should be included in the same family. All behavioral and ecological characters taken in concert suggest that the *Vireolanius* spp. are members of the Vireonidae.

SUMMARY

The Chestnut-sided Shrike-vireo, the largest vireonid and one of the few species with dimorphism in plumage color, occurs above 1850 m in the mountains of Mexico from San Luis Potosi south into the volcanic highlands of western Guatemala. We studied this species in northern Morelos in May 1972 and 1973 and in November of 1971 and 1972 in pine-oak forest in the mountains above 2880 m. Shrike-vireos were fairly common at both these sites.

Six vocalizations comprising both songs and calls were recorded in the field and then spectrographically analyzed. These vocalizations included: (1) primary song, a monosyllabic wailing whistle of the male; (2) short song, a non-musical song of the male; (3) *myaaaah*, a call given in an aggressive context; (4) distress calls, resembling those of other passerines; (5) contact calls, single low-pitched buzzy calls given by both sexes; and (6) buzz-rattles, which structurally resemble contact calls, given by both sexes.

Territories were as large as 4.1 ha and were defended against conspecifics by song and occasionally by physical combat.

The Chestnut-sided Shrike-vireo forages at heights between .6 and 30 m in trees and shrubs, taking arthropods from leaves and less frequently from bare branches and trunks. Some seeds and fruits are also eaten.

The first 2 nests known, found in northern Morelos, were quite large but nonetheless of typical, pensile, vireonid construction. Both sexes participated in nest-building, but the female did more of the work in the latter stages of construction. Construction took between 20 and 25 days. The male accompanied the female with song during this building and foraging. Copulation was seen once at Nest 1 at the end of building activities. The breeding season begins in late April, coinciding with the beginning of spring rains, and continues at least into mid-summer.

Behavioral similarities between *Vireolanius* spp. and other vireonids suggest that they are closely related and thus should be included in the Vireonidae.

ACKNOWLEDGMENTS

We are grateful for assistance in various ways from Drs. A. J. Baker, D. Barr, A. R. Emery, and A. R. Phillips. Ms. Maria Thinh prepared the figures. We thank the curatorial staff of the Bell Museum, University of Minnesota, for loan of the immature shrike-vireo. The Office of Dirección General de la Fauna Silvestre, Departamento de Conservacion, México, D. F. very kindly provided scientific permits. Research on vireos is supported in part by funds from the National Research Council of Canada.

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dept. of ornithology, royal ontario museum, 100 queen's park crescent, toronto, ontario m5s 2c6 (barlow and james), and dept. of zoology, univ. of toronto. toronto. ontario, canada (barlow). accepted 28 feb. 1975.

NEW LIFE MEMBER

George B. Reynard of Riverton, N.J. has recently become a life member of the Wilson Society. Dr. Reynard is employed as a research scientist at the Campbell Institute for Agricultural Research. While professionally Dr. Reynard is a botanist, his ornithological work in bioacoustics is well recognized. He has prepared record series on the bird songs of Puerto Rico, Jamaica, Hispaniola. and Cuba and has made special studies of the vocalizations of rails, owls, and caprimulgids. In addition to his sound recordings, Dr. Reynard has published papers dealing with this work and has developed a collapsible parabolic sound reflector for use in recording bird songs. Dr. Reynard is married and has 3 children and 2 grandsons.

TIME BUDGET OF BREEDING GADWALLS

Thomas J. Dwyer

Time budget studies have been made of birds as diverse as blackbirds (Orians 1961), wrens (Verner 1965), hummingbirds (Wolf and Hainsworth 1971) and finches (Schartz and Zimmerman 1971) but few accounts of duck time budgets have been published. Tamisier (1972) recently studied the activity rhythm of wintering European Green-winged Teal (*Anas crecca*). Klima (1966) described the activity rhythm of the European Pochard (*Aythya ferina*) and Folk (1971) added data on the Tufted Duck (*A. fuligula*). These authors were mainly concerned with detecting diurnal or nocturnal activity patterns and did not discuss how the division of time among various activities related to the reproductive strategy of the species. Titman (1973), however, did present data on the daily routine of Mallard (*Anas platyrhynchos*) pairs during the breeding season.

Dwyer (1974) studied the social behavior of the Gadwall (*Anas strepera*) and the importance of foraging activities to its territorial behavior. This paper will elaborate on that concept and demonstrate how the remaining activities relate to the reproductive strategy of pairs.

STUDY AREA AND METHODS

Data were gathered in 1973 in the glaciated prairie region of south-central North Dakota. The study area, 9.6 km south of Medina in west-central Stutsman Co., consists of rolling hills interspersed with small undrained depressions containing wetlands of various sizes and types. The number of wetland basins per square km ranges from 2 to 12 and they average 1.6 ha in size. Approximately 40% of the uplands is pasture and forage crops and 60% is small grain crops.

Gadwall pairs or lone males were observed with a 20× spotting scope or 7 × 35 binoculars during one-hour intervals in the daylight hours of April, May, and June, 1973. A metronome timing device (Wiens et al. 1970) set at a 15-sec interval was used to give a time base for recording activities. Each time the tone sounded the activity of both members of a pair or lone male was recorded. Two, one-hour sampling periods were picked at random during 3 separate time periods of the day, 06:00–11:00, 11:00–16:00, and 16:00–21:00 hours. I attempted to observe a pair for one full hour in each of the 3 time periods each day. Inclement weather, farming activities, or unavailable birds prevented fulfillment of this goal approximately one-half of the time. Observations where made on a variety of pond types over a 41.4 sq km area. An energy budget was constructed for male Gadwalls by extrapolation from time budget data in order to examine the costs of defense of the female during the breeding season.

For purposes of data analysis I split the breeding season into 3 phases: spring arrival, prenesting, and laying. Pairs in flocks were considered to be in the spring arrival

phase until the second week of May. After that date, pairs showing intraspecific intolerance and obviously not in flock situations were judged to be in the prenesting phase. Gadwalls show more synchrony in the start of nesting than most ducks (Duebbert 1958, Oring 1969). Nest records and brood observations on the study area in 1972 and 1973 showed that most hens began nesting the last week of May. Thus, I could be reasonably sure that birds were in the prenesting phase until the latter part of May. Observations were made of 2 pairs in the laying phase. I could identify each drake by plumage characteristics and I confirmed that the females were laying by watching them fly to the nest while the drake remained on the pond alone.

I did not use data resulting from less than 30 min of continuous observation. Thirteen hours of observations made during the spring arrival period were not picked at random. Data for the prenesting and laying phase totaled 34.8 and 23.4 hours, respectively. Six hours of data were also gathered on lone males waiting for their laying females. Paired or unpaired *t* tests, as appropriate, were used to test for differences between means and statistical significance was inferred when $P < 0.05$.

The activities of the birds were categorized as follows:

Feeding.—This activity was recorded only when a bird was actually ingesting food obtained by surface or subsurface feeding. Birds sometimes swam short distances and immediately began feeding again. The time involved in changing location was coded as locomotor activities.

Resting.—This activity included sleeping and loafing on the water or shore of a pond.

Locomotor activities.—Swimming and walking on the shore of a pond or in shallow water were included in this category.

Comfort movements.—This category included all activities involved with body maintenance such as preening and bathing.

Threat postures.—Open-bill threat postures by males and Chin-lift postures (Lorenz 1953) by pairs or males involved in intraspecific encounters were recorded in this category.

Three-bird chases.—This activity involved aerial pursuit of a paired female by a paired male followed by the female's mate.

Alert.—Pairs normally stop all activities and assume a head upright posture when they are disturbed by other birds, farm machinery, or road vehicles. This behavior is common in a mated drake during prenesting and laying when his female is feeding, even when a disturbance is not present.

Out-of-sight.—Pairs or lone males were occasionally shielded from view by vegetation for short periods of time. Calculations of percentage of time spent in various activities were based on the amount of time birds were actually observed.

RESULTS

Seasonal activity of pairs.—The average amount of time paired Gadwalls spent in various activities during the spring arrival, prenesting, and laying phases is presented in Fig. 1. Females spent most of their time feeding during all 3 phases of the breeding season. During the spring arrival phase, feeding rates were remarkably similar between members of pairs (Fig. 1). Male feeding rates began to decline as soon as birds became

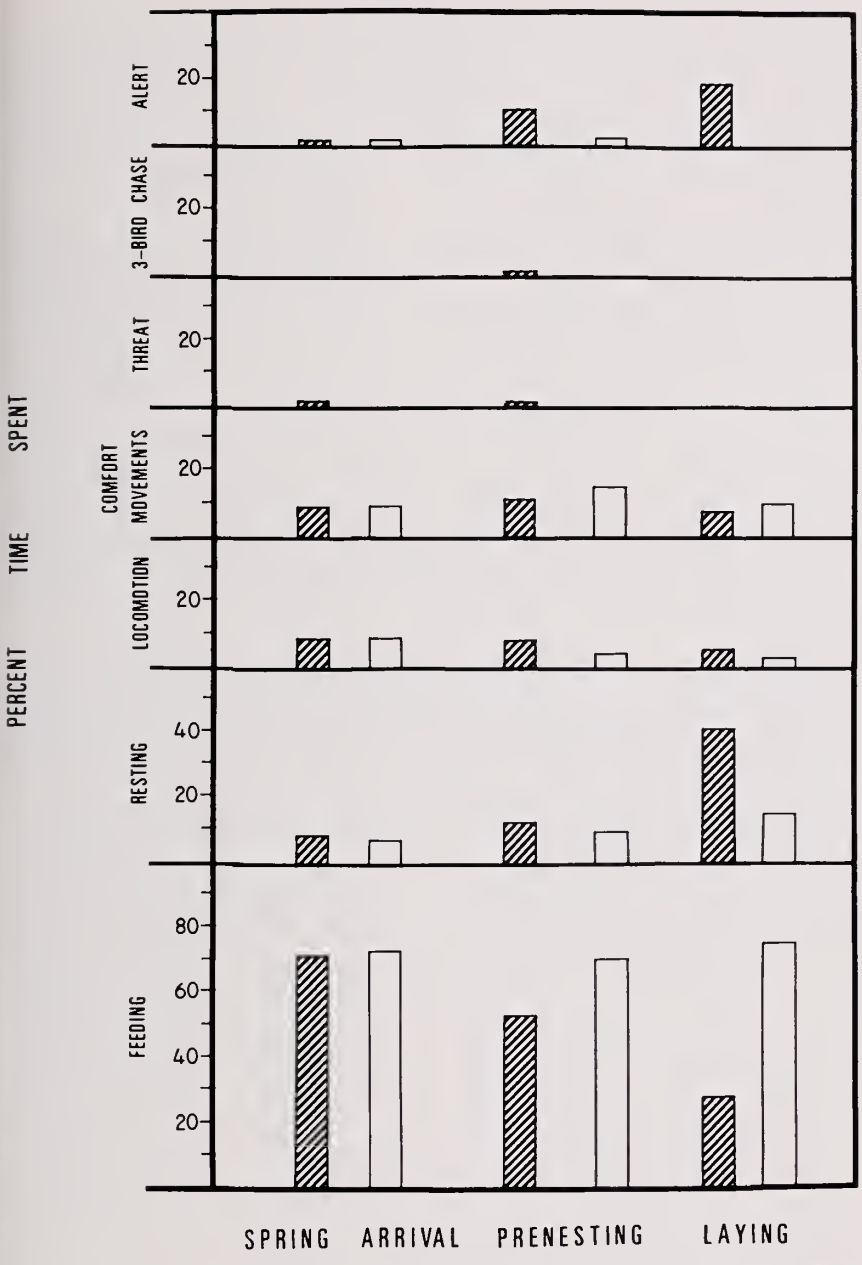

Fig. 1. Percent of time spent in various activities by pairs of Gadwalls. Males are indicated by crosshatching, females are unshaded. Percentages of less than 0.5 are not shown.

established on activity centers during the prenesting phase. Feeding rates for prenesting and laying females were significantly greater than for their mates. The average length of feeding bouts (the length of time during which only feeding activities were coded) for females averaged 6.9, 3.3, and 7.2 min during spring arrival, prenesting and laying, respectively, whereas male feeding bouts averaged 6.6, 1.9, and 0.9 min during the same time periods.

Time spent in resting activities was relatively constant for males and females during the spring arrival and prenesting phase but increased markedly in the males during the laying phase. Comfort movements consumed relatively constant amounts of time for males and females during all 3 phases. Locomotor activities consumed a smaller amount of time for both sexes as the season progressed.

The percentage of time paired males spent in threat postures decreased from 1.4% during spring arrival to 0.7% during prenesting and to 0.4% during laying. This decrease reflects the isolation pairs maintain from other pairs and unmated drakes as the season progresses. The amount of time spent by paired males in 3-bird flights, however, reached a maximum during prenesting and was significantly greater in this phase than in the laying phase.

Males and females spent similar amounts of time in an alert posture during the spring arrival phase. During prenesting and laying, paired males spent a significantly greater amount of time in an alert posture than did females. Males also spent a significantly greater amount of time in an alert posture during laying than during prenesting.

Daily activity patterns of pairs.—If the data are partitioned among the 3 daily time periods for the prenesting and laying phases, relatively few hours are available for analysis in each period. However, some general trends are evident. Neither males nor females changed feeding rates significantly during the day. However, female feeding rates were significantly greater than their mates regardless of the time of day. Male and female resting activities increased during the midday hours. Locomotor activities consumed the least proportion of the time in the evenings for females while no similar trend was noted for males in this activity. Comfort movements were relatively constant for females during laying but were highest in the morning during prenesting. No general pattern of comfort movements could be determined for males. Agonistic behavior or alert postures by males did not depend on the time of day but rather on the presence of other birds on the same pond or nearby farming operations.

Activities of lone males.—Drakes fed 27% of the time while with their hens but increased feeding rates to 36% of the time when they were alone.

TABLE 1

ESTIMATED ENERGY BUDGET OF MALE GADWALLS DURING 3 PHASES OF THE BREEDING SEASON

Activity	Spring Arrival		Prenesting		Laying	
	% day	Cost (kcal/bird per day)	% day	Cost (kcal/bird per day)	% day	Cost (kcal/bird per day)
Resting	5.83	4.41	9.85	7.46	28.35	21.47
Feeding	50.69	95.98	37.91	71.78	19.22	36.39
Locomotion	6.14	9.30	5.84	8.85	4.20	6.36
Comfort movements	6.26	7.11	8.33	9.46	5.38	6.11
Threat postures	0.97	2.20	0.49	1.11	0.31	0.70
3-bird chase	0.02	0.17	0.53	4.66	0.18	1.58
Alert	0.92	1.04	7.88	8.95	13.19	14.98
Nighttime	29.17	44.18	29.17	44.18	29.17	44.18
Total	100.00	164.39	100.00	156.45	100.00	131.77

Locomotor activities by drakes increased significantly from 6% to 15% when their females were absent. Drakes also spent significantly less time in the alert posture while alone than when they were with their females (5% versus 19%).

Energy budget of male Gadwalls.—Using the equation given by Lasiewski and Dawson (1967) for non-passerines, the standard metabolic rate for Gadwall males was computed as 76.7363 kcal/bird per day (using a mean weight of 0.955 kg taken from an April and May trapped sample of 7 males). The data in Fig. 1 are based on the percentage of daytime observation time and must be corrected by multiplying by 70.83% for the 7 hours of nighttime when no data were taken.

To convert the time budget data to an energy budget, several assumptions must be made. Feeding was given a value of 2.5 times resting because Gadwalls usually feed on or under the surface of the water while swimming. Locomotion was assumed to demand twice the standard metabolic rate (Prange and Schmidt-Nielson 1970) and comfort movements were given a value of 1.5 times the standard rate. Threat was given a value of 3 times resting because Gadwall males usually perform threat displays while swimming. Orians (1961) estimated the metabolic cost of displays of blackbirds to be 2 times resting. Three-bird chases were given a value of 11.6 times resting, based on Prange and Schmidt-Nielson's (1970) estimate

of the maximum sustained metabolic rate of a flying Mallard. A Gadwall drake's metabolism while involved in a vigorous 3-bird chase must be close to that value. Alert was given a value of 1.5 times resting. Nighttime activity was assumed to have the same energy cost as daytime locomotion because Gadwalls are active at night and are known to feed actively at times (Swanson and Sargeant 1972). The estimated energy budget for male Gadwalls during the spring arrival, prenesting, and laying phases of the breeding season is given in Table 1. These data should be viewed as a rough approximation since the effects of temperature on metabolic rate were not taken into consideration.

DISCUSSION

Pairs establish an activity center on a pond during the prenesting phase and spend virtually all the daylight hours of each day at this location until nesting begins (Gates 1958, Dwyer 1974). Paired Gadwall drakes show 2 types of defense against intruders in their activity centers (Dwyer 1974). The response toward an unpaired male or males who attempt to court his female takes the form of the Chin-lift posture or open-bill threat display. The Mutual Chin-lift posture of the pair preceded by Inciting by the female is also common in this situation. This is usually sufficient to cause an unpaired male to leave the activity center. If he persists, he will be attacked by the paired male and driven away. Paired males react to other pairs nearing the activity center by instigating a 3-bird chase. Females of pairs are vigorously chased for periods of up to 1 min and over linear distances of 1.6 km.

Competition for activity centers becomes intense during the first part of May. Each pair attempts to gain possession of an area where the female can localize her activities, begin to feed intensively, and build up her metabolic reserves for nesting (Dwyer 1974). Apparently other pairs are able to recognize potentially fertile areas which are at times in short supply. I have seen the drake of an established pair chase the same pair away as many as 6 times before the intruding pair moved on. The time spent by paired Gadwall males in 3-bird chases declined significantly from 0.7% during the prenesting phase to 0.3% of the time during laying. Thus, the maximum effort toward territorial defense is expended to establish a pair on an activity center before laying is initiated. Milne (1974) postulated that the feeding efficiency of the female European Eider (*Somateria mollissima*), prior to laying, was a very important determinant of her ability to breed successfully. He also stated that the constant attentiveness of the paired male was important in allowing the female to increase her food intake.

Costs of defense.—Because unpaired drakes are not competing for activity centers it seems logical in terms of energetics for a paired male to spend less effort defending against them than against another pair. Thus, threat postures suffice. Other pairs, however, could compete directly for the activity center and thus must be driven completely away. Similarly, Wolf and Hainsworth (1971) found different modes of defense in tropical hummingbirds depending on the position of the intruder in the hierarchy of competitors.

Paired males expend a relatively large amount of energy during prenesting maintaining isolation for their females in activity centers (Table 1). They are able to do this even though feeding for less time than during spring arrival, probably because of increasing food resources due to higher ambient temperatures and longer photoperiod. Verner (1965) showed that male Long-billed Marsh Wrens (*Telmatodytes palustris*) spent proportionally less time feeding as the season progressed because of increasing temperature and photoperiod. Feeding rates of males whose females are laying can drop even further because less energy is required for defense at that time. Thus, it appears economically feasible in terms of time and energy for paired males to protect their females and thereby maintain exclusive feeding areas for their use.

Females obviously need to ingest a tremendous amount of food to maintain themselves as well as mobilize the energy needed to produce a clutch averaging over 9 eggs. King (1973) estimated that egg production in ducks required an increase of 50–70% above the daily energy intake needed for the maintenance level of metabolism. Thus, their feeding rates must remain high during prenesting and laying. Differences in availability of foods in different ponds could change feeding rates to some extent, but the pattern described above probably would remain the same.

SUMMARY

Time budgets for pairs of Gadwalls during the breeding season were calculated based on 71.2 hours of observation. Feeding occupied the greatest proportion of the time of female Gadwalls during the spring arrival, prenesting, and laying phases of the breeding season. Feeding rates for prenesting and laying females were significantly greater than for their mates regardless of the time of day. The percentage of time paired males were involved in agonistic encounters other than 3-bird chases decreased from 1.4% during spring arrival to 0.4% during laying. Paired males, however, spent a maximum amount of time in 3-bird chases during the prenesting phase. Feeding rates did not change significantly for males or females during the day in the prenesting or laying phase.

Gadwall drakes apparently use more energy defending their females from the approach of pairs than from unmated drakes because pairs could directly compete for an activity center. Mated drakes help assure the reproductive output of the pair

by maintaining an exclusive feeding area for the female before and during the time of egg formation.

ACKNOWLEDGMENTS

D. Alan Davenport wrote the computer program to summarize the data. I especially thank Douglas H. Johnson for editorial and statistical advice. Gary L. Krapu and George A. Swanson reviewed the manuscript. The Bioelectronics Laboratory of the James Ford Bell Museum of Natural History, University of Minnesota, constructed the metronome timing device.

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northern prairie wildlife research center, jamestown, nd 58401.
accepted 10 jan. 1975.

REQUEST FOR ASSISTANCE

Color-marked Swainson's Hawks.—Nestling Swainson's Hawks have been fitted with red, green, or blue vinyl patagial wing markers in the Columbia Basin of southcentral Washington. The markers are crescent shaped and will be visible on flying and perching birds. These markers will contain the symbol X or A followed by 2 numerals (e.g. X08, A23). Each hawk will have a single patagial marker on its right wing.

Post-fledging behavior, migration, and nest site selection are several of the more important points being studied.

Should you see any of these birds, please write—Richard Fitzner, Ecosystems Department, Battelle Northwest Laboratories, Richland, WA 99352. Include date, time of day, and location of the observation, plus name of observer(s), color of marker, and if possible, the numbers printed on the marker. Also include the number of Swainson's Hawks associated with the marked individual(s).

BREEDING BIOLOGY OF THE BOREAL CHICKADEE

Margaret A. McLaren

The reproductive biology of some species of North American chickadees (Paridae) is well-known (Odum 1941a, 1941b: Bent 1946: Brewer 1961); however there have been no detailed studies of the breeding behavior of the Boreal Chickadee (*Parus hudsonicus*), a species of the northern coniferous forests. This paper presents both quantitative and qualitative information about the breeding behavior of the Boreal Chickadee, from the stage of early pair formation to the dispersal of the young.

STUDY AREA AND METHODS

Field observations were made in Algonquin Provincial Park, Nipissing District, Ontario, from April through July in 1971 and 1972. The major tree species of the study area are white spruce (*Picea glauca*), black spruce (*P. mariana*), and balsam fir (*Abies balsamea*), but there is some interspersion of trembling aspen (*Populus tremuloides*) and white birch (*Betula papyrifera*).

Approximately 1500 hours were spent observing birds or nests. Data were recorded in a notebook or taped. Hatching dates were obtained by inspecting the nest cavity; when this was impossible, these were estimated within 1 or 2 days on the basis of the behavior of the male, which changes markedly at the hatching of the young. In all cases, either fledging was observed, or young known to have been in the nest the previous day were seen in the nearby trees a day later. Some birds were individually recognizable by plumage characteristics, but many were not; most of the latter were caught and individually marked with colored leg bands. I marked 8 adult and 13 juvenile chickadees.

RESULTS AND DISCUSSION

Flock break-up, pair formation, and territoriality.—Pair bonds in the Boreal Chickadee develop gradually as winter flocks break up. With the onset of warmer weather aggressive activity within the flock increases, with chases and supplanting attacks occurring frequently. Chases fall into 3 categories. In the most common type (A), the sex of the participants cannot be determined by their behavior. Birds of either sex fly from the vicinity of the aggressor when attacked. As the season advances a second type of chase (B) becomes evident. Some birds, presumably females nearing breeding condition, merely move 2 to 3 m when attacked by a male. This behavior is similar to that observed by Hinde (1952) in the Great Tit (*Parus major*) and by Brewer (1961) in the Carolina Chickadee (*P. carolinensis*).

Although females usually withdraw only a short distance when attacked, a third type of chase (C) was observed on 5 occasions. These chases always began near the top of a tree; from there the pair spiraled downward, flying

rapidly around the tree with the male 15 to 20 cm behind the female. On 4 occasions the male gave one or several musical calls (McLaren, in prep.) while chasing, and in all 5 instances the chase ended with the female giving solicitation calls. Although I could never see the birds at the end of any of these chases, I do not believe copulation occurred. My reasons for this interpretation are that the birds reappeared almost immediately and I never heard the calls usually given by a mounting male. Whether such chases do actually play a part in pair formation is difficult to say. Two chases, which took place within an hour of each other, involved birds apparently already paired, as they had been together on the territory for more than a week. The other 3 chases were in flock situations.

The most striking characteristic of type C chases was the constancy of the distance (about 20 cm) between the birds in flight over a distance of 3 to 4 m. By comparison, in type A chases, which often proceeded downward through one tree and were frequently accompanied by musical calls from the male, the 2 birds were occasionally as close as 15 to 20 cm: usually they were farther apart, and typical chases never ended with solicitation.

Hole inspection may play some part in pair formation in this species. On 20 April 1972, a banded male, in a flock of 4 birds, flew to the stub of a broken branch in a white birch and was followed by a female, his mate of the previous year. Thereupon the male flew away, whereas the female made 4 excavating trips, carrying wood chips out of the cavity each time. She then rejoined the remaining birds, but the male made another flight to the prospective nest hole before returning to the flock. After 10 min this flock flew across a river and was not further observed intact. Later in the day, the same male and female were found together in their territory of the previous year. Brewer (1961) suggests that hole inspection in the Carolina Chickadee, if involved in pair formation at all, is of importance only after the pair has been associated for a time. There is considerable evidence that *Parus* species mate for life (Hinde 1952), and this seems likely the case in the Boreal Chickadee. My only color-banded pair in 1971 was again mated in 1972.

Once a pair separates from the flock, a pre-nesting period elapses before nesting behavior begins; this period is of variable duration, depending upon whether the pair was formed in late April or not until early May. The paired birds forage close together, usually on the ground where melting snow has revealed material dropped from the trees, and occasionally in trees—most frequently in the upper third.

After the members of a pair have been associated for 2 to 3 weeks and have established a territory, the female begins to beg food from the male. Begging behavior is characterized by specific calls and often by wing fluttering. Wing fluttering consists of vertical movements of the wings as they are

held slightly away from the body. Begging by the female in the presence of the male continues until hatching of the eggs, a period of 4 to 5 weeks. Begging in this species may be advantageous to the female during incubation in terms of her energy expenditure. Krebs (1970) has shown that in the Blue Tit (*P. caeruleus*), a female receives 2.5 times as much food when fed by the male as when foraging for herself.

Once a pair has been formed, it may either immediately establish a territory or wander for a short time before settling in an area. The use of vocalizations to advertise ownership of a territory in this species is debatable, but pairs defend their territories by use of vocalizations, as well as by chasing and supplanting attacks. Chases vary widely from rapid aerial twisting and turning, to slower flights in which rivals remain 3 m or more apart. Physical contact was not observed in territorial conflicts. Chasing and calling continue up to 15 min, after which, as in lower intensity encounters, one or both pairs move away. After retreat by one pair, the remaining pair flies from branch to branch and vocalizes at an accelerated rate for 5 to 10 min. These birds then return to their quiet foraging activities. The latest date that a territory was seen to be defended was 4 July 1971, by a male whose young had fledged 25 June 1971. This prolonged encounter was not intense, and chases were not close or rapid.

Territories in the study area were larger than 5 ha. As territories are seemingly not advertised vocally, boundaries are undoubtedly frequently trespassed. Unless the resident male actually encounters the interloper, nothing comes of the intrusion. In 2 instances, I followed an unbanded pair for more than 15 min through the territory of another pair without their being detected and attacked. Undetected intrusions may also occur in other species that have large territories and do not regularly patrol them, such as in the Gray Jay (*Perisoreus canadensis*) (D. Strickland, pers. comm.).

Nest site selection, hole excavation, and nest construction.—Hinde (1952) indicates that it is advantageous for a species to be able to occupy suboptimal as well as optimal nest sites, so that reproduction occurs even though nest sites are not ideal. Perhaps this helps explain why Boreal Chickadees explore many holes of varying suitability that they find early in the season. At first, both sexes merely inspect holes, but within a few days the females begin to make excavation trips. Males do not at first show as much interest in excavation as females and often wander away giving *chickadee* calls. The female either follows him away or remains at the hole, also giving *chickadee* calls. Within a few days both sexes excavate with equal intensity. Unlike Black-capped Chickadees (*P. atricapillus*) (Butts 1931) and Carolina Chickadees (Tanner 1952), Boreal Chickadees apparently do not tend to nest in the same tree in succeeding years, as none of the 6 nest sites studied in 1971 were

occupied in 1972; nor were 2 other sites found in 1961 and 1969 reused (H. Scott, pers. comm.).

Softness of the heartwood rather than a preference for a specific species of tree seems to determine nest site choice. Of 22 nest sites used and/or excavated, all were in trees or stumps in which the heartwood was soft from rotting but the outer layers and bark were still hard. The length of time required for completion of the cavity apparently depends on how soft the wood has become. In some cases a bird enters a hole and immediately emerges carrying chips or pieces of rotted material (up to 3 cm long), repeating the activity 4 or 5 times in succession. When the wood is harder, a bird may spend 40 to 50 sec inside the hole hammering with its bill before carrying chips out. One pair dug a cylindrical hole 20 cm deep and 5 cm in diameter in a day, whereas another pair worked for 10 days in harder wood to complete a cavity 15 cm deep. Interestingly, even after a hole has been partially excavated as a nest, the pair may not nest there. Once, a hole was excavated for 5 days and then deserted.

In most North American chickadee species, the entrance hole is on the side of the nest stub (Odum 1941b, Brewer 1961). However, Gabrielson and Lincoln (1959) noted that the Boreal Chickadee seems to choose stumps with the hole facing upwards. I found 9 of the 22 more or less permanently selected cavities with this orientation. This differs significantly (χ^2, $P < 0.05$) from observations by Odum (1941b) of Black-capped Chickadee nests where only 1 of 18 had the entrance in this position.

In my study one bird excavated appreciably more than the other, and this was the female in all cases where the sexes were distinguishable (5 of 11 cases). The number of times different males entered their holes ranged from about 2 to 25% of the trips observed. Known females never departed the hole without carrying excavated material, whereas males made apparent "inspection trips" or merely hammered without bringing material out.

Despite the apparent abundance of holes in Algonquin Park, there is some interspecific competition for them. Red-breasted Nuthatches (*Sitta canadensis*) twice displaced excavating Boreal Chickadees, once appropriating a hole for their own use. Black-capped and Boreal chickadees, which were not found to be interspecifically territorial, did not compete for nest holes. In one case, Black-capped Chickadees nested successfully in a hole excavated, but then abandoned, by Boreal Chickadees.

Although neither all European *Parus* nor all North American titmice regularly excavate holes (Hinde 1952), all North American chickadees do (Bent 1946). When Boreal Chickadees select a site lacking a hole, the initial excavation behavior closely resembles that described by Brewer (1961) for Black-capped and Carolina chickadees in this situation. The bird hammers

some chips loose with its bill and drops them to the ground with shakes of the head. Shortly, the Boreal Chickadee begins carrying chips some distance from the nest site; these it usually inserts among the needles of a conifer with a few pushes of the bill, rather than simply dropping them as in the other 2 species. Other trees may also be used for deposition of chips such as leafless yellow birch (*Betula alleghanensis*) and northern white cedar (*Thuja occidentalis*); from these sites the chips immediately fall. I suggest that arboreal deposition of chips is stereotyped behavior in *P. hudsonicus*.

Upon completion of the cavity, Boreal Chickadees may either begin the nest immediately (4 of 6 cases) or allow several days to elapse before starting it. In 1972, perhaps owing to the lateness of the spring, one bird excavated and built a nest concurrently, entering the cavity with nesting material and a minute or 2 later departing with chips. The female alone builds the nest. As in other *Parus* species (Hinde 1952), the cavity forms the structural part of the nest, with the soft material merely serving as a mat for the eggs and young. Nesting material, consisting of plant down, animal hair, strands of fruticose lichen, and similar material, does not seem to be brought in any particular order. Egg-laying generally begins after 2 or 3 days of nest-building, but small quantities of nesting material may be brought as late as the first few days of incubation.

Both excavation and nest-building show rhythmic characteristics. Both birds excavate, or the female builds, for a period usually not exceeding 45 min; then both birds depart. While the female builds, the male remains nearby, where he calls occasionally, forages, or watches the female. Absence from the cavity rarely exceeds 1 hour except during the period after the cavity is complete and before the female has begun to build the nest. In this period the pair may visit the nest site only 2 or 3 times a day and excavate briefly. When the female returns to the nest after a protracted absence, she brings nesting material from wherever she has been in the territory; subsequent material is gathered within about 10 m of the nest.

Copulation and egg-laying.—Sixteen copulations were observed totally or in part. Copulation may be initiated by either the male (4 of 12) or the female (8 of 12). Typically, the sequence begins with solicitation calls and wing-quivering by one of the pair. (Wing-quivering is similar to wing-fluttering but the movements are more rapid and of smaller amplitude.) If the second bird is not immediately receptive, calling may continue as long as 40 sec. If the mate is ready to copulate, it responds with wing-quivering. The response of females also includes solicitation calls; these were not heard from responding males. The male mounts the female for no more than 2 sec, during which time he may give 1 of 3 different calls (14 of 16 cases) or not call. After the male dismounts, one or both birds may continue to give solicita-

tion calls and wing-quiver for several seconds before returning to normal activities.

In European *Parus* species, fighting in a pair may occur immediately before or after coition, but aggression does not seem to be an important part of the copulatory sequence itself (Hinde 1952, Stokes 1960). Among North American species, Boreal, Carolina, Black-capped, and Mountain (*P. gambeli*) chickadees use calls associated with aggression during copulation (pers. obs., Brewer 1961, Dixon et al. 1970). The Black-capped Chickadee apparently calls only prior to mounting, whereas Boreal and Mountain chickadees both give aggressive calls while mounted.

In both years I observed coition in several different pairs subsequent to their first nesting. Apparently no birds raised second broods, and only in 1971 did any pairs excavate cavities or build nests after their first nesting.

Egg-laying always began before the nest was complete. In the 2 cases in which it could be determined, an egg was laid daily before 06:00. Incubation began on the day of laying the ultimate or penultimate egg. Prior to the beginning of incubation, the eggs were covered by nesting material when the female was away from the nest ($N = 4$); once incubation had begun they were left exposed when she left.

Incubation.—The female alone incubates, and the male enters the nest only to feed her. Incubation behavior, as in many passerines, is marked by attentive periods (when the female sits on the eggs) and inattentive periods (when she forages, either alone or with the male). In 193.2 hr of observation the mean attentive and inattentive periods of 8 females were respectively: 32.9 min (range: 3 to 92) and 8.0 min (range: 1 to 41). The mates of these females fed them at the mean rate of 0.65 times per attentive hour (range 0.1 to 1.54. 120.9 hr of observation).

An attentive period may end either by the female departing alone or by the arrival of the male. When the male arrives at the nest, he perches on a nearby branch and calls softly. The female then comes to the nest entrance or she flies to a branch near the nest; in both cases she is fed by the male. When the female occasionally does not come up to the entrance when the male calls, he enters and feeds her; after that she may or may not follow h'm out of the cavity. In the first day or 2 of incubation, a male arriving at the nest when the female is absent enters and quickly leaves the hole several times. He may then leave, but usually he remains and feeds the female when she returns. The female then goes directly to the nest hole. After the first few days of incubation, the members of the pair appear to become synchronized, and the male arrives only when the female is present. One male came to the nest while the female was absent 4 times in the first 4 days of incuba-

Table 1

Lengths of Attentive Periods by Incubating Boreal Chickadees

	Length of period and sample size					
	When called by male			When not called by male		
Pair	Mean (min)	S.D. (min)	N	Mean (min)	S.D. (min)	N
71-1	28.8	13.0	4	38.9	9.0	22
71-2	33.4	24.0	8	31.9	9.3	9
71-3	15.4	9.5	10	28.5	12.0	10
71-4	27.8	10.6	23	33.0	0	1
72-1	28.6	15.2	9	34.2	15.6	18
72-2	22.7	5.9	4	36.3	16.7	27
72-3	28.6	12.9	5	44.1	13.1	24
72-4	24.4	7.3	4	33.8	13.3	25

tion (9 hr of observation), but never again in the female's absence (19 hr of observation).

If the female leaves the nest when the male is not present, she flies across the territory giving loud *chickadee* calls. If she encounters the male, she stops calling, begs for food and is fed by the male. If the female does not encounter the male, she forages on her own. A female leaving with the male continually begs throughout the inattentive period. Whether she is with the male or not, she returns to incubate suddenly, flying swiftly and directly to the nest.

Odum (1941b) suggested that the male Black-capped Chickadee influenced the length of incubation bouts, because attentive periods of the female were shorter when she emerged in response to his calls than when she emerged spontaneously. Table 1 shows a similar and significant relationship in 7 of 8 Boreal Chickadees (Wilcoxon matched-pairs signed-ranks test, $P < 0.01$, 1-tailed). As I studied attentive periods at all times of day in each third of the incubation period, if there was variability in period length as a function of time of day or phase of the incubation period, it would be unlikely to bias the data on attentive period length.

Weather seemingly affected the length of attentive periods to a certain extent. In very cold weather attentive periods tended to be longer, but this was by no means absolute. For example, on 10 June 1972 the high temperature was 5° C. Two attentive periods of one female were shorter than her mean incubation period, and 2 were longer. However, all 5 inattentive periods the same day were shorter than average.

In my study the incubation period ranged from 11 to 16 days, with most eggs hatching at 15 days. This is slightly longer than the incubation period of other North American chickadees. The incubation period in the Black-capped Chickadee is 11 to 13 days (Forbush 1929), in the Carolina Chickadee 11 (Bent 1946) or 12 (Tanner 1952) days, and in the Mountain Chickadee 14 days (Wheelock 1904). Eggs in a clutch frequently did not all hatch on the same day, and in one case 3 days were required for complete hatching.

As far as I could determine, the female ate the egg shell. Twice there were only eggs at one inattentive period and a hatched young at the next inattentive period. In neither instance was the egg shell observed in the nest after the female left, nor was it carried out by her.

Nestling stage.—In the first few days after hatching of the young, the female continues to alternate attentive and inattentive periods: she sometimes, but not always, brings food back to the young when she returns from an inattentive period. Once the young have hatched, the behavior of the male changes markedly in that he brings food far more frequently. In addition, the female exits from the nest far more often when he calls.

As Brewer (1961) observed in the Carolina Chickadee, in Boreal Chickadees brooding attentiveness is about the same as incubation attentiveness in the first 3 days after hatching. After this, brooding declines rapidly and is discontinued by about the 11th day (the day of cessation varies individually). In some pairs, the female still enters the hole and remains 3 or 4 min at a time even on the day before fledging; other females remain for only a few seconds to feed the young from the 11th day.

A behavior pattern apparently not reported in other parids is "nest watching" by the female after cessation of brooding. The female sits on a branch 1 to 5 m from the nest, where she preens, looks around, or rests, while the male does most of the feeding of the nestlings. This behavior was especially noticeable at 3 of 9 nests, and at another nest I observed it on 4 occasions in the 5 days before fledging. In the last case, the bird spent only a few minutes at a time watching, rather than periods of 15 to 20 min spent by the other 3. Potential predators were not chased by watching females, although they were scolded.

The amount of food brought to the young increases as the nestling period progresses. Table 2 gives the rate of feeding, as well as the rate of fecal sac removal, at this time. At first the male does most of the feeding and may continue to do so through fledging; however, in the last 3 or 4 days before fledging, both adults may share equally in feeding.

When a male and female arrive at the nest together, both wing-flutter but usually do not call. Either may enter the nest first, and the other waits for the first to emerge before entering. When the male arrives alone, he often

Table 2

Care of Nestlings by Adults

	Stage of nestling life and sample size					
	Days 1–5	Hours of observation	Days 6–10	Hours of observation	Days 11–18	Hours of observation
Total feedings per hour[1]	9.1	53	12.2	129	13.9	60
Feedings per hour per chick[1]	1.7	40	2.2	27	2.8	45
Percent of feedings by male	73.2	53	62.8	65	56.9	45
Fecal sacs removed per hour per chick[1]	0.03	40	0.24	27	0.34	45

[1] By both adults.

gives soft calls; on the other hand, the female rarely calls as she approaches the nest. If a bird flies directly into a nest already occupied by its mate, the former bird immediately comes out again and waits for the mate to emerge.

The modal length of the nestling period is 18 days. Again this is longer than 17 (Bent 1946) or 13 to 14 (Dixon 1961) days for the Carolina Chickadee or 16 days for the Black-capped Chickadee (Odum 1941b). The young cannot fly earlier than this, although by the 15th day they can flutter-walk (run along the ground and sometimes up tree trunks while flapping their wings) well enough to make their capture (by a human) difficult. At least 4 young (out of a brood of unknown size) that fledged on the 15th day survived to at least 10 days after fledging.

In 3 cases in which fledging was actually observed, it took place in the morning: these fledglings could fly at least 3 m on their first attempt. During fledging, both parents flew or hopped rapidly about the nest area, giving frequent soft calls. If there was a lag between the fledging of various of the young, the adults continued to feed those still in the nest. The earliest fledging took place 22 June 1971 while the latest was 3 July 1972. Once all the young had fledged the family departed the vicinity of the nest.

Dispersal of the young.—For the first 2 weeks after fledging, the family essentially stays within the boundaries of the nesting territory. During this time the young are fed with decreasing frequency by their parents. For the first few days the young do not move about much, spending most of their time sitting quietly and giving occasional begging calls. The volume and frequency of these calls increases as an adult approaches. In time the fledglings increasingly forage on their own, with a concomitant decrease in

begging. Within a week after fledging, the fledglings seemingly fly as well as adults. By 3 weeks after fledging the young have left the territory.

SUMMARY

The breeding biology of the Boreal Chickadee was studied in the summers of 1971 and 1972 in Algonquin Park, Nipissing District, Ontario.

Pair formation develops gradually, beginning while birds are still in the flock. Male-female chases (3 types) and hole-inspection may play a part in pair formation, but this is not certain. Begging behavior apparently does not play an important role in pair formation in this species, as it does not occur until after the pair has been associated for 2 to 3 weeks and has established a territory. Excavation of cavities may occur at several holes before a nest site is chosen. Although both sexes excavate, the female alone builds the nest, which consists of soft plant and animal material. The cavity forms the structural part of the nest. Copulation may be initiated by either sex, and the calls given by the male while mounted suggest an aggressive component to this activity. The female alone incubates and is fed largely by the male. She incubates for shorter attentive periods when called from the nest by the male than when terminating an attentive period spontaneously. Hatching occurs about the 15th day. Both parents feed the young, with the male feeding more at the beginning of the nestling period; both sexes feed more or less equally by fledging. Some females show a behavior not reported in other parids, i.e. "nest watching." The young fledge on about the 18th day of life and are fed with decreasing frequency for about 2 weeks. After this they are no longer found regularly in the nesting territory.

ACKNOWLEDGMENTS

My thanks to Dr. D. W. Dunham under whose direction this study was carried out in partial fulfillment of the M.Sc. degree at the Dept. of Zoology, University of Toronto. Dr. J. C. Barlow provided constructive criticism of earlier drafts of the manuscript. I am indebted to the Ontario Ministry of Natural Resources for allowing me to work in Algonquin Park.

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NEW LIFE MEMBER

Eric G. Bolen has recently become a life member of the Wilson Ornithological Society. Dr. Bolen is presently assistant director of the Welder Wildlife Foundation, Sinton, Texas, and has just recently been named editor of the Wildlife Society Bulletin. Dr. Bolen is interested in waterfowl ecology, endangered species, and eagle-livestock predator-prey relationships as well as the general ecology of birds. He has published nearly 50 papers resulting from his research. In addition to his professional interests, Dr. Bolen collects antiques, especially decoys. He is married and has one son.

A CHRISTMAS COUNT ANALYSIS OF WOODPECKER ABUNDANCE IN THE UNITED STATES

Carl E. Bock and Larry W. Lepthien

The science of biogeography ideally includes consideration of both the distribution and density of species. Traditionally, biogeographers have studied only the ranges of species, because of difficulties inherent in measuring population densities over broad geographic areas. On the other hand, animal ecologists (e.g., Andrewartha and Birch 1954, MacArthur 1972) have suggested that those same environmental factors which control the distribution of a species also affect its pattern of abundance within that distribution.

Woodpeckers are among the best known groups of North American birds. Nearly all of the 20 species found north of Mexico have received careful attention. We know where they occur and we know in general what foraging strategies they employ. However, few studies have attempted to determine large-scale patterns of population density.

The National Audubon Society Christmas count data, published as local population censuses, are of varying quality, but collectively are of such magnitude as to reveal continent-wide population phenomena. In this study we have used Christmas count data to analyze some patterns of winter abundance of North American woodpeckers, with a goal of revealing more about the ecology and adaptation of the species than would be possible from simple analyses of their distributional limits.

METHODS

This study represents a continuation of our efforts to use Christmas count data to study large-scale patterns of avian ecology and biogeography in North America. We described details of data storage, retrieval, and analysis previously (Bock and Lepthien 1974).

For this investigation we selected 27 inland regions in the U. S. (Fig. 1), based on the map and descriptions of Küchler (1964). For some areas (especially in the West) we had to combine many of Küchler's vegetation units to form a "region" (Fig. 1, Table 1) which contained even a marginally sufficient number of Christmas counts for meaningful analysis. When possible we combined similar vegetation types, so that each region consisted of generally similar habitats. The regions we analyzed were of varying shapes and sizes—often very complex configurations—designed to correspond when possible with Küchler's units of potential vegetation (see legend of Fig. 1). The 19 woodpecker species included in this analysis are listed in Table 1.

Christmas count data were extracted in groups of counts which fell inside the different regions. The average number of individuals observed per party-hour was computed as a measure of the relative abundance of each woodpecker species within each area. The results of Christmas counts probably are biased in that they underestimate species where

FIG. 1. Locations of vegetation regions used to analyze the winter abundance of woodpeckers in the U.S. 1 = everglades; 2 = southern mixed forest; 3 = southern floodplain; 4 = oak-hickory-pine; 5 = southern Appalachian oak; 6 = oak-hickory; 7 = mixed mesophytic forest; 8 = northern Appalachian oak; 9 = beech-maple; 10 = northeastern mixed forest; 11 = Great Lakes mixed forest; 12 = northern Minnesota coniferous; 13 = mesquite-acacia; 14 = central Texas savannah; 15 = central shortgrass prairie; 16 = bluestem prairie; 17 = ecotone of 16 and 9; 18 = northern shortgrass prairie; 19 = Arizona mixed forest; 20 = warm desert; 21 = southern Rocky Mountain mosaic; 22 = central Rocky Mountain mosaic; 23 = Great Basin; 24 = northern Rocky Mountain coniferous; 25 = interior Calif.; 26 = Sierra Nevada; 27 = northwestern mixed forest. These regions are based as closely as possible upon the classification of Küchler (1964).

they are common and overestimate them where they are rare. We do not feel that this would seriously influence our findings, since these possible biases would minimize real differences and not create artificial ones. However, Christmas count coverage is relatively poor in montane regions of the West; here, rare species may be missed entirely. For example, neither the White-headed Woodpecker nor the Northern Three-toed Woodpecker were observed in region 24, even though both occur there. We feel that the major value of this analysis is to reveal patterns in the more abundant and widespread species.

Avian data were taken from 827 counts published in the Christmas count issues of *American Birds* for the years 1969–70, 1970–71, and 1971–72. Climatological data are 50-year means from U.S.D.A. (1941); primary productivity estimates are from a combination of Whitaker (1970) and Collier et al. (1972).

ABUNDANCE OF SPECIES

Table 1 shows the average number of each woodpecker species divided by total party-hours of effort for counts in the 27 regions. The data suggest that the Common Flicker is the most abundant woodpecker wintering in the

areas we analyzed. It is followed by the Downy, Red-bellied, Hairy, and Acorn woodpeckers. These species are ubiquitous except the Acorn Woodpecker, which had a high average only because it reaches extraordinary densities in California, and the Red-bellied Woodpecker, which is very common throughout much of the eastern half of the U.S. (Table 1).

Habitat preferences of species with restricted distributions are apparent from Table 1. Several widely distributed species require further analysis. Figure 2 shows very generalized maps of their abundances constructed from the data in Table 1. Since our 27 regions did not include all of the U.S., and since Christmas counts may not detect species where they are rare, these maps should not be considered as depicting exact limits of distribution. They do, however, give a picture of relative abundance for the more ubiquitous species. Four degrees of shading were used to indicate increasing densities within each species; they do not represent similar densities between species (see Table 1).

Hairy and Downy woodpeckers.—These resident species are widely distributed, but show a marked concentration in the northeastern quarter of the U.S. (Fig. 2a,b).

Ladder-backed Dendrocopos.—The resident Red-cockaded, Ladder-backed, and Nuttall's woodpeckers occupy the southern and western U.S., and appear to replace their relatives concentrated in the northeastern states (Fig. 2c). However, none of these ladder-backed species reaches the densities of Hairy and Downy woodpeckers (Table 1), a fact which figures significantly in the abundance pattern of the *Dendrocopos—Picoides* group as a whole.

Common Flicker.—More than any group shown in Fig. 2, the Common Flicker concentrates in winter at lower latitudes (Fig. 2d). It is more common in relatively open habitats (Table 1) than would be expected on the basis of latitude alone.

Red-headed Woodpecker.—This species shows greatest winter densities in the Midwest, but also is common in the lower Mississippi Valley and the Southeast (Fig. 2e).

Red-bellied Woodpecker.—This species is abundant in the Midwest, the Mississippi Valley, and the Southeast (Fig. 2f). It and the Yellow-bellied Sapsucker are the only woodpeckers reaching high densities in peninsular Florida.

Pileated Woodpecker.—This species is unusual in that it occurs in both coniferous and broadleaf forests (Fig. 2g, Table 1). Highest densities are found in the same areas as the 2 previous species.

Yellow-bellied Sapsucker.—This species has migrated from the Great Basin, northern Rocky Mountains, and northern plains by the time Christmas counts are conducted (Fig. 2h). Small numbers remain in the northeastern

Table 1

Winter Abundance of Woodpeckers in Major Vegetation Regions in the U.S. (see fig. 1), based on 827 Christmas Counts.[1]

Species	Region (number of counts)													
	1 (15)	2 (22)	3 (22)	4 (36)	5 (34)	6 (24)	7 (15)	8 (60)	9 (25)	10 (106)	11 (106)	12 (15)	13 (4)	14 (14)
Common Flicker (*Colaptes auratus*)	.21	.88	1.47	.83	.15	.78	.42	.17	.45	.13	.06	.004	–	1.07
Pileated Woodpecker (*Dryocopus pileatus*)	.03	.16	.26	.08	.11	.28	.19	.02	.03	.02	.04	.06	–	–
Red-bellied Woodpecker (*Centurus carolinus*)	.51	.55	1.14	.72	.14	1.02	.35	.09	.44	.001	.24	.008	–	.10
Golden-fronted Woodpecker (*C. aurifrons*)	–	–	–	–	–	–	–	–	–	–	–	–	1.24	.35
Gila Woodpecker (*C. uropygialis*)	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Acorn Woodpecker (*Melanerpes formicivorus*)	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Red-headed Woodpecker (*M. erythrocephalus*)	.001	.13	.49	.18	.03	.22	.09	.01	.43	.001	.22	.02	–	.05
Lewis' Woodpecker (*Asyndesmus lewis*)	–	–	–	–	–	–	–	–	–	–	–	–	–	.004
Yellow-bellied Sapsucker (*Sphyrapicus varius*)	.15	.20	.24	.35	.06	.22	.05	.02	.01	.002	.004	.003	.04	.05
Williamson's Sapsucker (*Sphyrapicus thyroideus*)	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Hairy Woodpecker (*Dendrocopos villosus*)	.002	.03	.18	.09	.11	.28	.23	.28	.16	.68	.50	.53	–	.01
Downy Woodpecker (*D. pubescens*)	.01	.08	.61	.48	.40	.97	.99	1.18	1.09	1.09	.88	.93	–	.14
Ladder-backed Woodpecker (*D. scalaris*)	–	–	–	–	–	–	–	–	–	–	–	–	.47	.36
Nuttall's Woodpecker (*D. nuttallii*)	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Red-cockaded Woodpecker (*D. borealis*)	.001	.03	.03	.06	–	–	–	–	–	–	–	–	–	–
Arizona Woodpecker (*D. arizonae*)	–	–	–	–	–	–	–	–	–	–	–	–	–	–
White-headed Woodpecker (*D. albolarvatus*)	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Black-backed Three-toed Woodpecker (*Picoides arcticus*)	–	–	–	–	–	–	–	–	–	.001	–	–	–	–
Northern Three-toed Woodpecker (*P. tridactylus*)	–	–	–	–	–	–	–	–	–	.001	–	.004	–	–

TABLE 1. (*Continued*)

Species	Region (number of counts)													$\bar{X}$
	15 (21)	16 (23)	17 (98)	18 (25)	19 (5)	20 (23)	21 (18)	22 (29)	23 (12)	24 (6)	25 (14)	26 (9)	27 (13)	
Common Flicker (*Colaptes auratus*)	1.04	.22	.70	.03	.80	.61	.49	.27	1.73	.33	1.32	1.60	1.10	.62
Pileated Woodpecker (*Dryocopus pileatus*)	–	.005	.03	–	–	–	–	–	–	.02	–	.02	.03	.05
Red-bellied Woodpecker (*Centurus carolinus*)	.07	.04	.81	–	–	–	–	–	–	–	–	–	–	.23
Golden-fronted Woodpecker (*C. aurifrons*)	–	–	–	–	–	–	–	–	–	–	–	–	–	.06
Gila Woodpecker (*C. uropygialis*)	–	–	–	–	.30	.40	–	–	–	–	–	–	–	.03
Acorn Woodpecker (*Melanerpes formicivorus*)	–	–	–	–	.17	–	.08	–	–	–	.55	3.14	.30	.16
Red-headed Woodpecker (*M. erythrocephalus*)	–	–	.56	–	–	–	–	–	–	–	–	–	–	.09
Lewis' Woodpecker (*Asyndesmus lewis*)	–	–	–	–	–	.001	.05	.05	–	–	.02	.33	.26	.03
Yellow-bellied Sapsucker (*Sphyrapicus varius*)	.008	.001	.03	–	.05	.03	.03	–	–	–	.04	.06	.08	.06
Williamson's Sapsucker (*Sphyrapicus thyroideus*)	–	–	–	–	.003	–	.003	–	–	–	–	.01	–	<.01
Hairy Woodpecker (*Dendrocopos villosus*)	.06	.33	.25	.22	.003	.03	.16	.08	.002	.11	.01	.04	.07	.16
Downy Woodpecker (*D. pubescens*)	.22	.81	1.42	.30	–	.002	.004	.09	.01	.19	.06	.15	.28	.46
Ladder-backed Woodpecker (*D. scalaris*)	.03	–	–	–	.33	.08	.02	–	–	–	–	–	–	.05
Nuttall's Woodpecker (*D. nuttallii*)	–	–	–	–	–	–	–	–	–	–	.17	.16	.006	.01
Red-cockaded Woodpecker (*D. borealis*)	–	–	–	–	–	–	–	–	–	–	–	–	–	.01
Arizona Woodpecker (*D. arizonae*)	–	–	–	–	.02	–	–	–	–	–	–	–	–	<.01
White-headed Woodpecker (*D. albolarvatus*)	–	–	–	–	–	–	–	–	–	–	–	.10	.002	.01
Black-backed Three-toed Woodpecker (*Picoides arcticus*)	–	–	–	–	–	–	–	–	–	–	–	–	–	<.01
Northern Three-toed Woodpecker (*P. tridactylus*)	–	–	–	–	–	–	–	.01	–	–	–	–	–	<.01

[1] Data are expressed as the average number of birds observed per party-hour of effort.

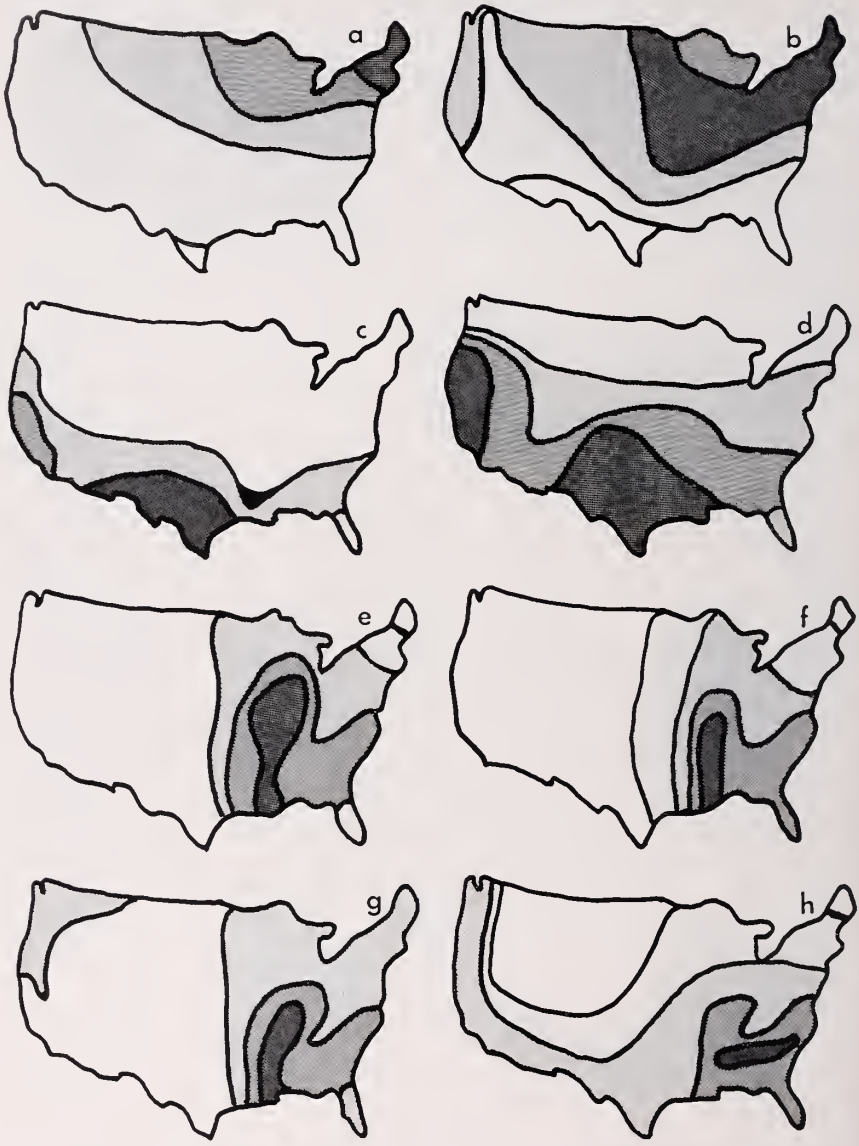

FIG. 2. Winter abundance patterns of common woodpecker species. White areas = no birds observed; the darker shadings indicate increasing densities within species, but are not comparable between species (see Table 1). a = Hairy Woodpecker; b = Downy Woodpecker; c = ladder-backed *Dendrocopos*; d = Common Flicker; e = Red-headed Woodpecker; f = Red-bellied Woodpecker; g = Pileated Woodpecker; h = Yellow-bellied Sapsucker.

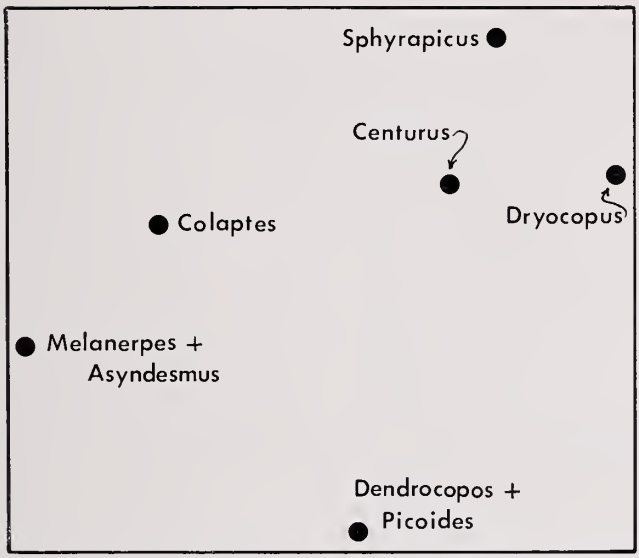

FIG. 3. Two-dimensional ordination of 6 woodpecker taxonomic groups, based on similarities of distribution and abundance in winter in the U.S. The axes have no specific meaning, but the distances between points are inversely proportional to the similarities of distribution and abundance patterns (see Beals 1960).

states and the Midwest (see Tate 1973), but the greatest concentrations are, again, the Mississippi Valley and especially the Southeast—including peninsular Florida. Of course many sapsuckers winter south of the U.S. (Howell 1952, 1953). *Sphyrapicus varius ruber* of the Pacific Northwest is a resident subspecies, and *S. v. daggeti* winters along the Pacific Coast. Our data suggest that these sapsuckers are less abundant than the eastern *S. v. varius*.

SIMILARITY OF TAXONOMIC GROUPS

Data on woodpecker species were combined to provide information on the distribution and abundance patterns of 6 woodpecker taxonomic groups; *Dendrocopos* and *Picoides* were treated as one group, because of their general similarity, as were *Melanerpes* and *Asyndesmus*. The other four groups were *Colaptes*, *Sphyrapicus*, *Dryocopus*, and *Centurus*. We carried out a similarity analysis and 2-dimensional ordination of the groups, based upon similarities of their abundance patterns in the 27 regions analyzed (see Beals 1960 for techniques). The closer the groups are shown in the ordination (Fig. 3), the greater the similarity of their abundance patterns. Results of this analysis show that: (1) *Centurus* is most nearly intermediate to all of the other groups in terms of its abundance pattern. (2) *Dendrocopos—Picoides* as a

Table 2

Correlation Coefficients Between Woodpecker Abundance and Environmental Characteristics[1]

	Average temp.	Maximum temp.	Minimum temp.	Summer precip.	Winter precip.	Primary productivity
Dendrocopos + *Picoides*	–0.41	–0.22	–0.50	0.42	–0.03	0.18
Melanerpes + *Asyndesmus*	–0.07	–0.10	0.00	–0.21	0.45	–0.07
Colaptes	0.23	0.24	0.36	–0.23	0.40	–0.10
Dryocopus	0.19	–0.04	0.16	0.40	0.35	0.60
Sphyrapicus	0.50	0.10	0.50	0.45	0.46	0.63
Centurus	0.65	0.36	0.53	0.41	0.06	0.50

[1] See methods for data sources. $N = 27$ for all calculations; r values $\geqslant 0.33$ are significant at the 0.05 level of probability.

group has by far the most distinctive abundance pattern. (3) *Sphyrapicus*, *Dryocopus*, and *Centurus* (because of the abundant Red-bellied Woodpecker) form a cluster, although all 6 groups are rather well spread. (4) *Melanerpes*—*Asyndesmus* is widely separated from all other groups except *Colaptes*.

We next measured a number of environmental parameters for each of the 27 regions, and computed correlation coefficients between these and the winter abundances of the 6 woodpecker groups (Table 2). These data may shed some light upon the ultimate causes of the configuration of abundance similarities shown in Fig. 3.

Dendrocopos—Picoides is the only group strongly negatively correlated with temperature regime. Northeastern populations of the Hairy and Downy woodpeckers are so large that they give the entire group a northern abundance pattern. This could be a reflection of the common circumboreal distribution and evolutionary history of these genera (see Short 1971).

Centurus, *Sphyrapicus*, and *Dryocopus* all are positively correlated with areas of higher temperatures, precipitation, and especially primary productivity. These are birds of wet, warm climates.

Colaptes and *Melanerpes* (plus *Asyndesmus*) winter in regions which are relatively unproductive, and where winter precipitation exceeds summer precipitation (Table 2).

DISCUSSION AND CONCLUSIONS

There appears to be a strong correlation between patterns of woodpecker abundance described in this study and published information on the feeding ecology of the species. Some of the major relationships of common species are discussed in the following paragraphs.

Dendrocopos.—The Hairy and Downy woodpeckers forage in winter largely by excavation (Kilham 1966, Lawrence 1967, Jackson 1970), and are so-adapted morphologically (Spring 1965). This explains their ability to live in areas where winters are severe and tree-surface insects scarce. By contrast, the ladder-backed *Dendrocopos* are more generalized foragers, relying to a greater degree in winter upon free-living insects (Ligon 1971, Short 1971, Miller and Bock 1972). These are species restricted to areas of warmer climate, where surface insects would persist in greater numbers all year.

Melanerpes—Asyndesmus.—The Acorn, Lewis', and Red-headed woodpeckers to varying degrees are dependent upon stored mast in winter (Kilham 1958a,b; Bock 1970; MacRoberts 1970). Red-headed Woodpeckers are most common in the Midwest (Fig. 2e), undoubtedly because of the abundance of oaks and corn in this region. Acorn Woodpeckers are more common in California than in the Southwest (Table 1), probably because acorn crops are larger and more predictable in California (Bock and Bock 1974a). Tables 1 and 2 indicate that *Melanerpes* and *Asyndesmus* winter most abundantly in areas which are relatively open and lacking in summer rains. This undoubtedly is related to the fact that all 3 species forage extensively in summer by flycatching. Summer requirements should have little to do with winter abundance patterns, but the Acorn Woodpecker is resident and the Lewis' and Red-headed woodpeckers, while often migratory, are highly opportunistic and will remain on or near breeding grounds if it is possible (e.g., Hadow 1973). Also, these species will flycatch on warm winter days.

Colaptes.—Flickers concentrate at lower latitudes in winter, and apparently prefer relatively open habitats (Table 1, Fig. 2d). Very likely this is due to their decided preference for ants which they take on open ground (Bent 1939, Dennis 1969). Areas of dense forest, and especially areas where snow often covers the ground, would be relatively unsuitable flicker habitat.

Dryocopus.—The Pileated Woodpecker is more restricted to mature, dense, and productive forests than any other considered here. In winter it relies heavily on carpenter ants excavated from partially decayed trees (Hoyt 1957). It is easy to see why it is most common in the moist forests of the Mississippi Valley and Southeast, where the maturation-decay process is relatively rapid. The virtual absence of Pileated Woodpeckers from the central and southern Rocky Mountains no doubt is due to the scarcity of dense highly productive forests in these regions compared to the Northwest or the Southeast (see Bock and Bock 1974b).

Sphyrapicus.—Tate (1973) recently reviewed the foraging ecology of the eastern Yellow-bellied Sapsucker. He made the significant observation that (p. 854) "northern wintering birds subsist on a diet of arthropods (mostly insects) obtained from the bark of trees, frozen fruit, and very little sap,"

whereas ". . . sapsuckers in the middle latitudes feed on local sap flow from many tree species." This specialized woodpecker clearly would be best suited to areas with milder winters and extensive, productive woodlands, where sap would be available all year. This conclusion is strongly supported by our data (Tables 1 and 2, Fig. 2h).

Centurus.—The 3 species of *Centurus* in the U.S. form no clear ecological pattern, perhaps because they are part of a much more diverse group of species occurring to the south (Selander and Giller 1963). *Centurus* woodpeckers are very generalized foragers, and also showed the most intermediate pattern of abundance of the genera studied (Fig. 3). The widespread *C. carolinus* appears to be particularly generalized among North American species. It does relatively little excavating (Cruz, in press), takes considerable vegetable material in winter (Bent 1939), and concentrates in winter in productive, warm areas (Table 2). It may store mast (Kilham 1963), but it does not appear to be nearly as specialized in this regard as *Melanerpes* or *Asyndesmus*.

SUMMARY

Analysis of Christmas count data for 27 inland regions in the U.S. revealed major patterns of woodpecker abundance. Data for 6 woodpecker taxonomic groups were subjected to ordination analysis. In general, abundance patterns correlated well with information on the foraging ecology of the species and genera.

Dendrocopos (plus *Picoides*) showed a strong northeastern abundance pattern due to the high densities of Hairy and Downy woodpeckers in that region. The Common Flicker is very abundant at lower latitudes and in relatively open habitats. The Yellow-bellied Sapsucker was concentrated in the Mississippi Valley and the Southeast. *Sphyrapicus varius varius* appeared much more abundant than the western subspecies. The Pileated Woodpecker was most abundant in forests of the Midwest and Southeast, and relatively rare in the West. The Acorn, Lewis', and Red-headed woodpeckers wintered where mast crops are available. Acorn Woodpeckers were much more common in California than in the Southwest; Red-headed Woodpeckers were abundant in the Midwest, where oaks and corn are available. *Melanerpes* and *Asyndesmus* forage extensively by flycatching, and are most abundant in open habitats, even in winter.

ACKNOWLEDGMENTS

We would like to thank the many students who have helped to develop the Christmas count data banks. J. Bock and A. Cruz read an earlier draft and provided helpful suggestions as to form and content. This study was supported by grant GB 36860 from the National Science Foundation.

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NEW LIFE MEMBER

John P. Ryder has recently become a life member of the Wilson Ornithological Society. Dr. Ryder is an Associate Professor in the Department of Biology at the Lakehead University, Thunder Bay, Ontario. He is interested in the breeding behavior and ecology of colonial birds and in age-specific differences in larid behavior and reproductive success. He has published nearly 20 papers resulting from his research activities. Dr. Ryder is presently Director of the Federation of Ontario Naturalists. In addition to his professional interests, Dr. Ryder enjoys snowshoeing and photography.

EVOLUTIONARY ASPECTS OF PARENTAL BEHAVIOR: DISTRACTION BEHAVIOR OF THE ALPINE ACCENTOR

David P. Barash

Most animals that demonstrate parental care also engage in behavior that increases their offsprings' chances of survival when confronted by a predator, often at the risk of injury or death to the parent itself. Such "altruistic" parental behavior ranges from concealment and immobility to outright attacks upon the predator. In addition, many birds characteristically perform "broken wing" distraction displays in which the parent lures the predator away from the nest area by apparently feigning injury. Much of the early literature on this phenomenon has concerned controversy as to the motivational state of the animal performing the display (Armstrong 1949), leaving virtually untouched the ultimate questions of evolutionary interest. In fact, these behaviors provide ideal opportunities for analysis using the recently-described concept of "parental investment" (Trivers 1972). This paper describes the distraction behavior of the Alpine Accentor (*Prunella collaris*), suggesting an evolutionary interpretation for the observed pattern and for a general, hypothesized distinction between altricial and precocial species.

METHODS AND RESULTS

I studied two nests of the Alpine Accentor in Vanoise National Park, Savoie, France, during June and July, 1973. The nests were located on the ground in an alpine meadow, 150 m NE of Le Vallon (altitude 2400 m). Nest 1 contained 4 eggs when discovered on 19 June; all hatched between 7–8 July. Nest 2 contained 5 eggs when discovered on 21 June; 4 hatched between 9–10 July (the fifth never hatched). The Alpine Accentor responds to the presence of a human intruder by engaging in a conspicuous distraction display—the female characteristically flies from her nest, settles on the ground at some distance, and occasionally extends one or both wings, quivering them as though injured, often uttering a high-pitched repetitive call. During a series of daily tests, I approached each nest at a slow walk at the same time each day, wearing the same outer garments. I recorded the distance from me to the nest at which the display was elicited (flushing distance) and the distance from the nest at which the bird initially landed immediately prior to performing the display (settling distance). The results are presented in Figs. 1 and 2. Despite some day-to-day variability for each individual and considerable variation in the absolute values from nest to nest, the trend in

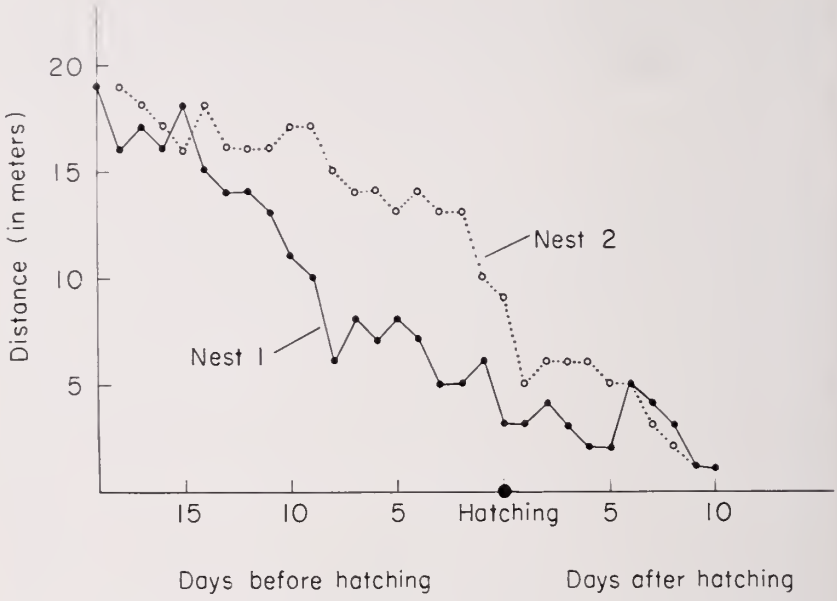

FIG. 1. Flushing distance of adult female Alpine Accentors as a function of clutch age.

both cases is for a progressive decrease in both flushing and settling distances continuing through hatching until observations were discontinued (both nests were destroyed by a red fox, *Vulpes vulpes*, on 18 July, approximately one week before fledging would have occurred).

I also categorized the initial responses of the female after settling as either type A—no wing extension, no threat; type B—one or both wings extended, no threat; or type C—one or both wings extended, threat exhibited. As used here, "threat" involves rapid opening and closing of the mandibles, often (but not necessarily) accompanied by vocalization. As with the decrease in flushing and settling distance described above, the transition from type A to C may be considered a progression of increasing intensity and conspicuousness, involving increased risk to the performer with a corresponding increase in the likelihood of successfully distracting a predator and thus saving eggs or nestlings. Table 1 reveals that as with settling and flushing distances, there is a progressive increase in display conspicuousness with increasing age of the eggs or nestlings. Thus, low initial frequencies of type C responses eventually increase, while high values of type A responses decrease with time. Dividing the sequence into 3 periods—19 to 10 days before hatching, 9 days before hatching to 1 day after, and 2 days after hatching to 10 days after—and combining the data for both nests in each period, I compared

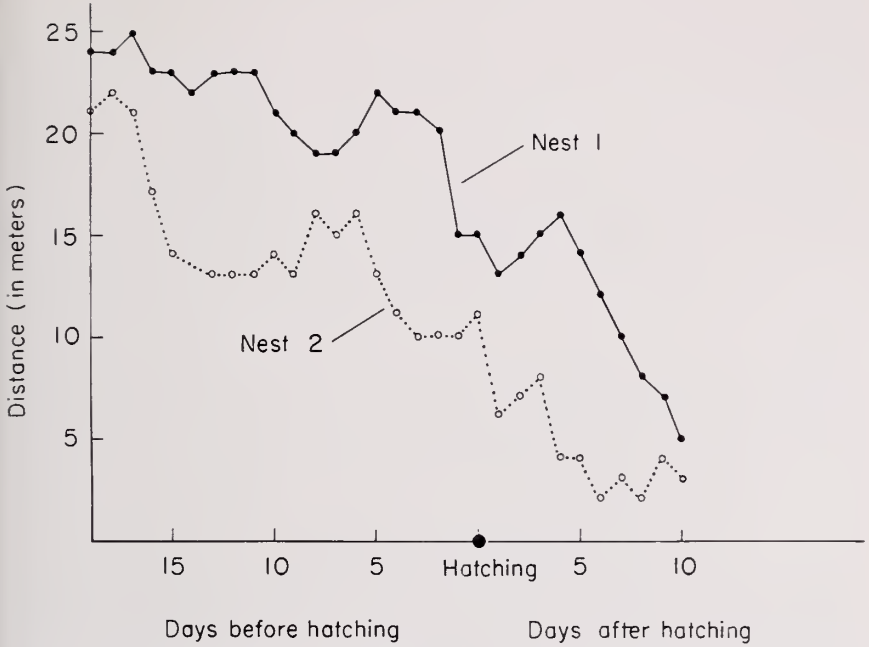

FIG. 2. Settling distance of female Alpine Accentors as a function of clutch age.

the observed frequencies of response types A–C with the frequencies that would be expected assuming equal representation of all 3 responses in each time period. A chi-square test demonstrated that the observed distribution deviated significantly from chance ($p < .01$).

DISCUSSION

Several workers have described a temporal pattern in avian distraction displays, all demonstrating increases in conspicuousness and intensity, peaking when the eggs hatch and declining thereafter (Simmons 1955, Stephen 1963, Gramza 1967). Armstrong (1956) and Gramza (1967) attributed this pattern to the increased conspicuousness of a nest with newly hatched young, reasoning that maximal efforts were required of the defending parent at that time. Armstrong (1956) went on to say that "It is broadly true that in passerines distraction display tends to be most intense when the young leave the nest, although exceptions occur, while in many other groups it is apt to be most accentuated about the time of hatching or when the young are a few days old."

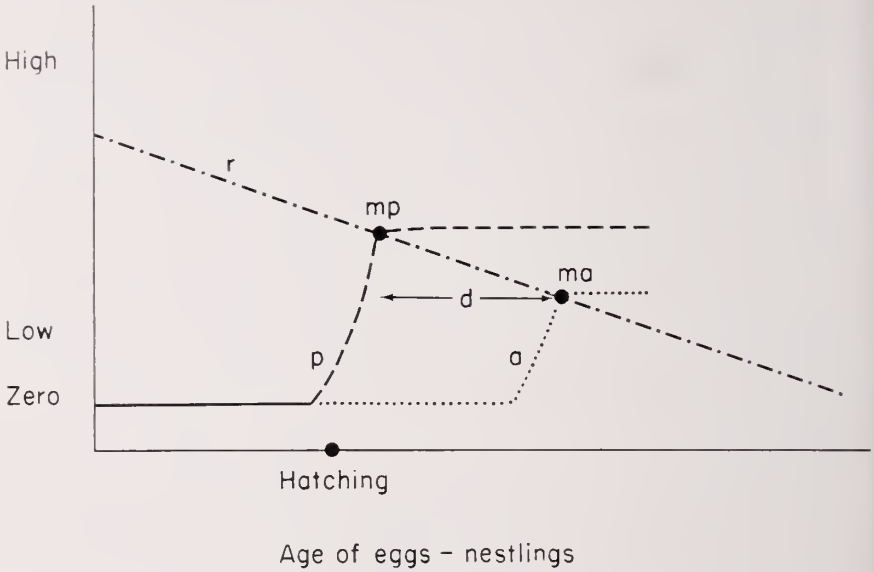

FIG. 3. Schematic representation of the relationship between evolutionary factors influencing distraction displays in precocial and altricial birds. r = probability of successful renesting by the parents; p = relative survival potential of precocial young in the absence of parental investment; a = relative survival potential of altricial young in the absence of parental investment; mp = maximum display by parents of precocial young; ma = maximum display by parents of altricial young; d = difference in time between maximum display by parents of precocial and altricial young. The sum of the ordinate values for "r" and either "p" or "a" at any age of the offspring represents the evolutionary return on the investment of parental distraction displays at that time. For precocial birds this sum is maximum shortly after hatching, while for altricial birds maximum return is received just before fledging.

Significantly, all of the above recent quantitative studies were concerned with non-passerine species having relatively precocial young, and all supported Armstrong's generalization by revealing an inverted U-shaped temporal pattern of display conspicuousness. My study involved a passerine, altricial species and demonstrated a different pattern, again consistent with Armstrong's generalization: display conspicuousness increased with increased age of the egg-nestling unit. This apparent difference in temporal patterning of display conspicuousness between precocial and altricial species may be interpreted as follows.

Trivers (1972) has defined "parental investment" as "any investment by the parent in an individual offspring that increases the offspring's chance of surviving (and hence, reproductive success) at the cost of the parent's ability to invest in other offspring." Insofar as increased conspicuousness

TABLE 1

RESPONSE TYPES OF FEMALE *PRUNELLA COLLARIS* AS A FUNCTION OF AGE OF HER CLUTCH (SEE TEXT FOR DESCRIPTION OF CATEGORIES)

	Days Before Hatching																			Days After Hatching										
	20	19	18	17	16	15	14	13	12	11	10	9	8	7	6	5	4	3	2	1	0	1	2	3	4	5	6	7	8	9	10
Nest 1	A	A	A	A	B	A	B	A	B	B	A	B	A	A	B	B	B	B	B	C	B	C	C	B	C	C	C	C	C	C	C
Nest 2	–	A	A	A	A	B	B	A	A	B	A	B	B	B	B	B	B	B	B	B	B	B	B	C	B	B	C	C	B	B	C	–

of a distraction display renders the performer more likely to be preyed upon while increasing the chances of its offspring's survival, performances of such behavior can be considered a form of parental investment. One might expect that the amount of such investment worth expending on any particular clutch would be to some degree a function of the amount already invested, and the older the egg-nestling unit, the greater parental investment it represents. This is especially true since the older the egg-nestling unit, the lower the probability of renesting by the parent whose distraction display was unsuccessful—perhaps because of insufficient conspicuousness (i.e., risk) by the defending parent. In effect, as their offspring grow older, even parents capable of renesting find their eggs increasingly placed in the one basket at hand. The parallel increase in display conspicuousness with increasing age of the offspring presented here for *Prunella collaris* is consistent with this interpretation.

But *P. collaris* is an altricial species, in which the chances that offspring will survive without parental assistance are virtually zero, with essentially no change until fledging. By contrast, shortly after hatching the offspring of precocial species have a finite chance of survival without parental assistance, and this survival potential increases rapidly within a few days. Thus, although young of precocial species resemble altricial young in that they represent accruing parental investment as they get older, this increasing investment is to some extent counteracted by their rapidly-acquired ability to survive without further parental investment.

Whereas the optimum time for maximum parental investment in altricial species should occur just before fledging, with progressive increases leading up to that maximum, the optimum time for maximum parental investment in precocial species should be just after hatching, when the young are old enough to represent a large investment, but not so old that they no longer benefit from further investment. As precocial young become increasingly mobile and able to secure their own protection, the ultimate parental risk involved in protecting them would exceed the return in protection received

and a progressive decline in such parental investment would therefore be expected (Fig. 3). The differing temporal patterns of distraction displays reported for precocial and altricial species thus conforms to the predictions of evolutionary theory, using the concept of parental investment as a guide.

Possible habituation of the animals to the experimenter must also be considered. However, it would not explain the differential responses of precocial and altricial birds here reported. In addition, the progressive increase in response intensity shown in Table 1 runs counter to the expected performance of habituating animals. Thorpe (1951) has suggested that rapid habituation to a potential predator would be clearly maladaptive, and Gramza (1967) has proposed that repeated withdrawal of a human intruder might actually reinforce distraction behavior, just as the normally-occurring withdrawal of an owl is believed to reinforce mobbing of chaffinches (Hinde 1954). Finally, the very complexity of the human stimulus configuration plus the 24 hour interval between exposures both probably mitigate further against habituation.

Many considerations must influence the particular behavior patterns demonstrated by each species and broad generalizations may be deceptive. For example, the renesting capability of each species would have a profound effect upon its strategy of optimum parental investment. This factor is currently being investigated.

SUMMARY

The distraction display of the Alpine Accentor, a ground-nesting altricial species, increases progressively in conspicuousness and risk to the parent as the egg-nestling unit grows older. By contrast, precocial species appear to reach maximum display intensity around the time of hatching with progressive declines thereafter. This difference in temporal pattern is consistent with an evolutionary interpretation of behavioral strategies serving to maximize return on "parental investment."

ACKNOWLEDGMENTS

The observations reported in this study were made while conducting research on the social biology of the Alpine marmot (*Marmota marmota*) supported by an award from the US-France Exchange of Scientists Program, sponsored jointly by the National Science Foundation and the Centre National de la Recherche Scientifique. I am particularly grateful to the people of France and the U.S. for making this research possible, and to Monsieur Henri Contier, garde du Parc National de la Vanoise, for his friendship and for providing the information which eventually led to discovery of the 2 study nests.

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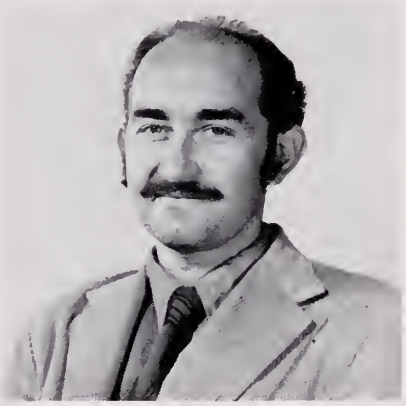
DEPTS. OF PSYCHOLOGY AND ZOOLOGY, UNIV. OF WASHINGTON, SEATTLE 98195.
ACCEPTED 1 JAN. 1975.

NEW LIFE MEMBER

Donald F. Bruning has recently become a life member of the Wilson Society. Dr. Bruning is presently Associate Curator of Ornithology at the New York Zoological Society in the Bronx, N.Y. His interests in ornithology include aviculture, behavior, and reproductive biology, and he has published over 25 articles in professional and popular journals dealing with his work. In addition to his professional interests, Dr. Bruning enjoys gardening and photography. He is married and has 2 children.



HABITAT USE AND FLOCK ACTIVITY OF DARK-EYED JUNCOS IN WINTER

Bradley M. Gottfried and Edwin C. Franks

Due to the relative severity of winters in the temperate regions of the United States, research pertaining to avian winter populations has been mainly limited to studies of home range size of passerines (Price 1931, Condee 1970), and dominance relationships among flocks at feeding stations (Sabine 1949). In addition, vegetational preference studies have been reported using brief observational methods (Quay 1947, Graber and Graber 1963, Johns 1971, Pulliam and Enders 1971). Few attempts (e.g., Robins and Raim 1970) have been made to follow the movements and activities of flocks for long periods of time, and thus gather data not possible using the above techniques.

We observed winter flocks of Dark-eyed Juncos (*Junco hyemalis*) that did not visit feeding stations to determine spatial and temporal changes in movements, habitat preference, and daily flock activity during winter.

METHODS AND MATERIALS

Junco flocks were observed frequently from 13 October 1971 to 25 March 1972 on 2 study areas in McDonough Co. west-central Illinois. Juncos were captured in mist nets and in baited walk-in traps from October to January. The nets were used on approximately 20 days and the traps were used on 5 days. All captured juncos were banded and backtagged for individual recognition. Four of the 11 juncos comprising flock I, and 4 of the 13 juncos of flock II were color banded and backtagged.

Flocks were generally observed for entire days (from the time of leaving the roosts in the morning until returning to the roosts in the evening) when temperatures were above 5°C, but at lower temperatures, observations were restricted to 3-hour intervals alternated with 2-hours of no observations. The cold-weather observation schedule varied from day to day so that each part of the day was sampled. Juncos were observed for 440 hours during the winter.

The percentage of time the juncos spent in each vegetation type was calculated as the amount of time spent there divided by the total observation time that the birds were not roosting.

Home ranges were plotted on aerial photographs obtained from the U.S. Soil Conservation Service. A compensating polar planimeter was used to determine the area of each home range.

Vegetation in the study area was classified into 7 types. *Short grass pastures* were those areas where grazing had reduced most herbaceous vegetation to less than 10 cm in height, although shrubs and taller forbs were also present. *Tall grass pastures* were lightly grazed areas where most vegetation was taller than 10 cm. *Mowed hay fields* were similar to short grass pastures except they did not include shrubs and forbs. *Forb areas* were abandoned fields in an early successional stage, with foxtail grass

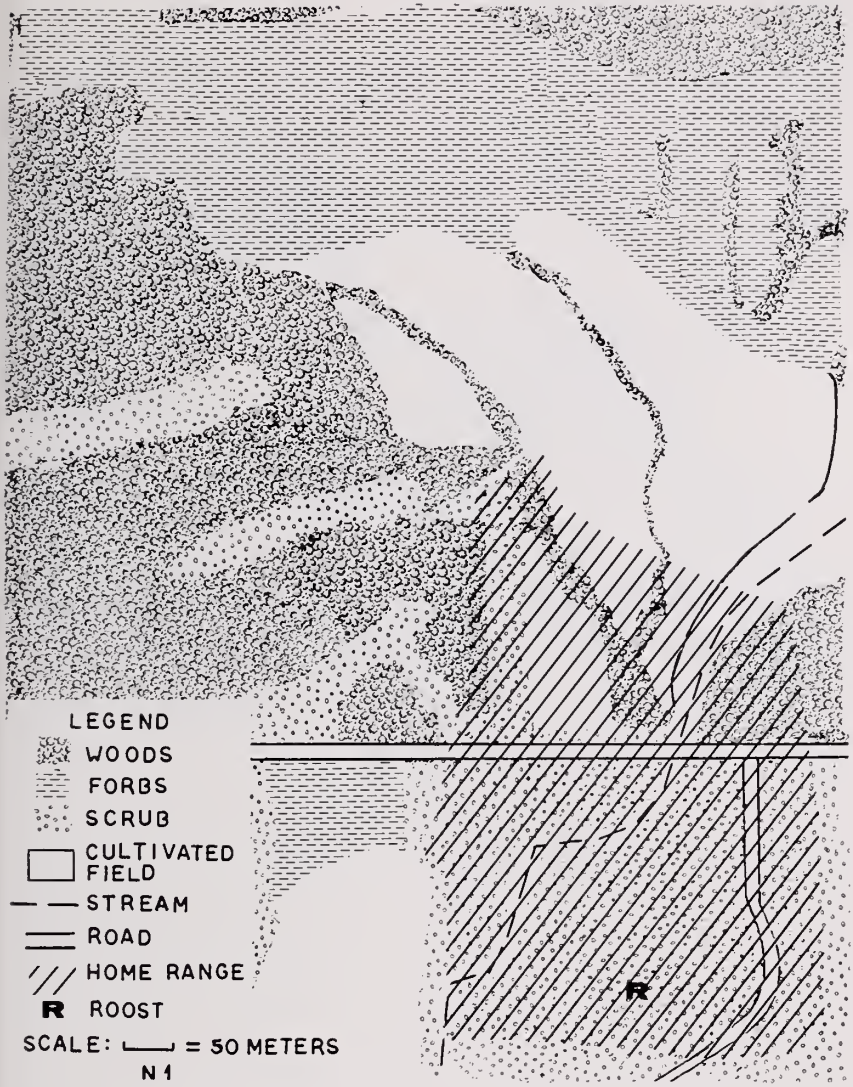


FIG. 1. Home range of flock I.

(*Setaria* sp.), asters (*Aster* sp.), and goldenrod (*Solidago* sp.). *Scrub areas* were fields in an advanced successional stage, with forbs, shrubs, and trees. *Woods* included irregular strips of mature trees along streams and larger areas with secondary growth of osage orange (*Maclura pomifera*), hawthorn (*Crataegus* sp.) and elm saplings (*Ulmus* sp.). *Cultivated fields* were the harvested stubble of soybeans (*Glycine max*) or corn (*Zea mays*).

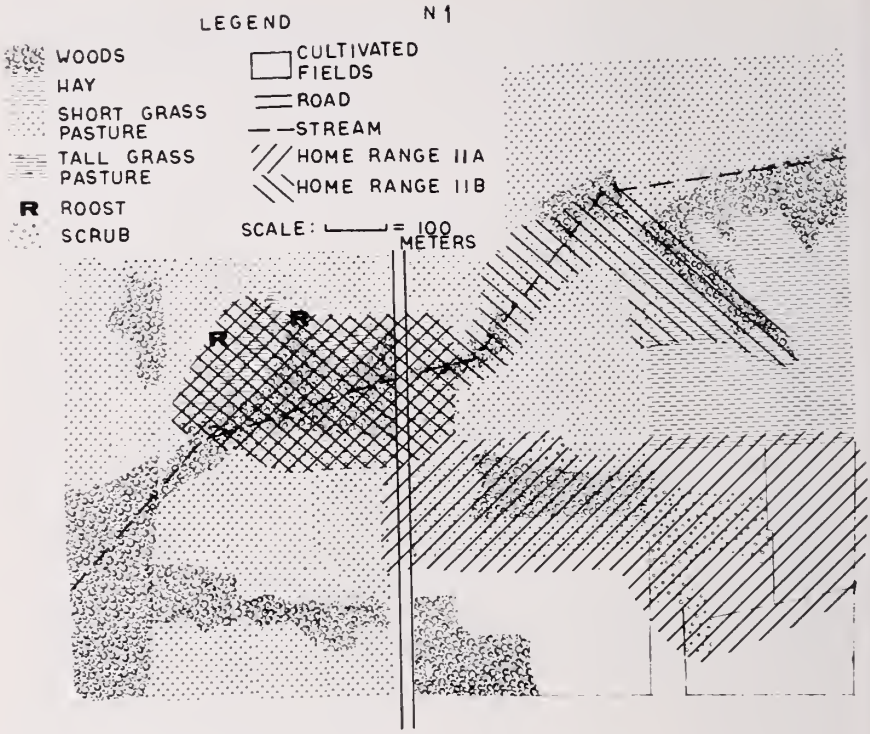


FIG. 2. Home range of flock II.

RESULTS

Winter Home Range.—The 11 juncos of flock I occupied study area I from 17 November 1971 until 14 January 1972, and restricted their activities to an area of 27 ha (Fig. 1). Flock II, composed of 11–13 individuals, used 2 home range areas (Fig. 2) in study area II during the winter. Winter home range IIA (33 ha) was used from the time of flock formation (mid-December) until 30 January when the flock broke up, apparently due to 10–15 cm of snow accumulation. When the snow melted a month later, the flock reunited (containing all 4 color-marked birds). For the remainder of the winter the flock used the same roosting areas (west of the road), but used a completely different feeding area (home range IIB, 17 ha). Vegetational composition of the home ranges is listed in Table 1.

For the first week after flock II broke up on 30 January, the members stayed in 5 groups of 2 to 4 birds, each group occupying a non-overlapping feeding area within the original home range. After the first week,

TABLE 1

PERCENTAGE OF EACH STUDY AREA AND HOME RANGE OCCUPIED BY VARIOUS HABITATS

Vegetation Type	Study Area I (90 ha)	Home Range I (27 ha)	Study Area II (110 ha)	Home Range II A (33 ha)	Home Range II B (27 ha)
Short grass pasture	0	0	40	20	40
High grass pasture	0	0	4	12	20
Cultivated fields	25	31	16	32	0
Scrub	20	40	4	15	3
Forbs	26	13	0	0	0
Woods	29	16	25	21	28
Hay fields	0	0	11	0	9

4 of the 5 groups abandoned their feeding areas, and congregated with other fringillids at nearby cattle pens, where stock feed was available on the ground. The 5th group remained in an area where a large tree prevented the accumulation of deep snow. During this period all of the banded birds continued to roost in the usual area.

All 3 winter home ranges had specific areas used day after day for certain activities. Each home range included a single area where intensive feeding occurred in the morning and late afternoon, as well as an area where most non-feeding activities occurred at midday. Scrub areas were used for intensive feeding by flock I. whereas short grass pasture was used by flock II. The midday non-feeding activities usually occurred in trees and shrubs adjacent to cultivated fields.

Diurnal habitat.—Dark-eyed Juncos generally fed in areas having trees, shrubs, or tall forbs, including short grass pastures, and soybean fields having boundaries of trees or shrubs. The birds flew to this taller vegetation when disturbed and perched there between feeding bouts. The occurrence of such vegetation probably determined to some extent the feeding areas used within the home range. Areas lacking taller vegetation (hay fields, and the centers of large cultivated fields) were rarely used; tall grass pastures were never used.

The junco flocks spent most of the day in scrub and short grass pastures where preening and perching activities predominated (Fig. 3). No other habitats were frequented by the juncos for even a quarter of their non-roosting hours.

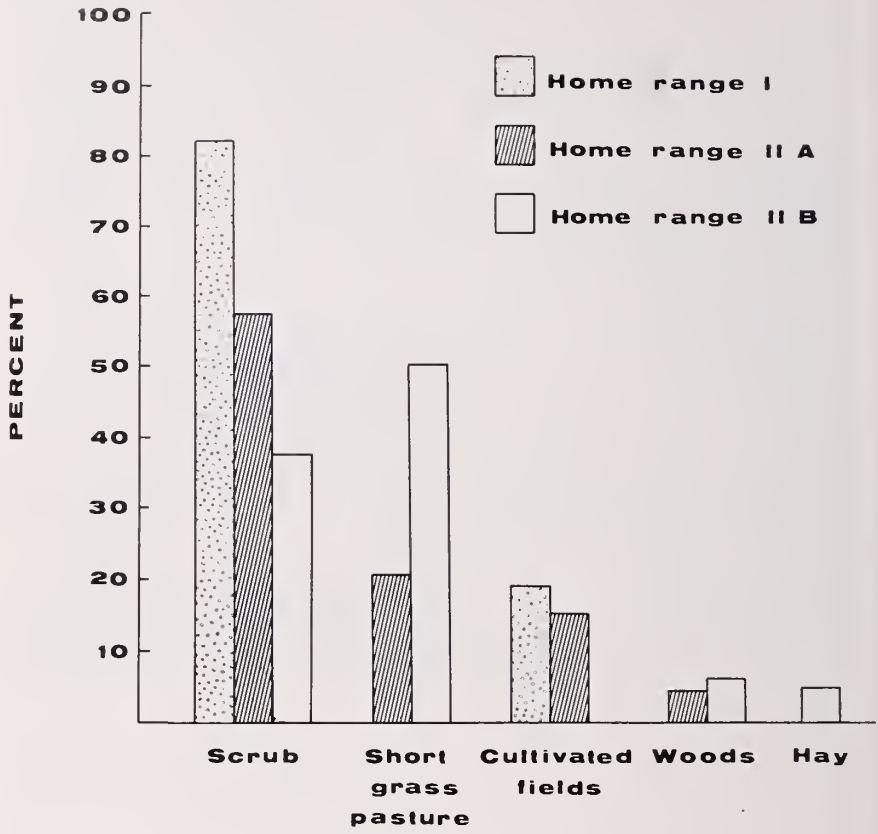


Fig. 3. Percentage of non-roosting time spent in each habitat.

Roosting habitat.—Juncos generally chose dense vegetation as roosting sites. On 10 December 3 members of flock I roosted in a red cedar tree (*Juniperus virginiana*), 3 on or near the ground in tall grass, 2 in osage orange thickets, and 2 in brush piles.

All members of flock II roosted in 2 adjacent jack pine (*Pinus banksiana*) plantations. They roosted 82–142 cm above the ground in trees 216–284 cm tall (Table 2). There was no relationship between the height of the roost tree and the height of the roost perch. The birds roosted in the part of each tree that had the densest foliage. The night temperature inside the dense foliage was generally only 1°C warmer than outside the crown, but wind velocity was substantially reduced by the foliage. A wind of 29 kph in the open was less than 1 kph at the roost site in 5 of the 7 trees.

TABLE 2

TEMPERATURE AND WIND CONDITIONS AT JUNCO ROOST SITES IN JACK PINE

Height of tree (cm)	Height of roost (cm)	Temperature (°C)		Wind (kph)	
		inside canopy	outside canopy	inside canopy	outside canopy
216	91	–3.9	–3.3	calm	29
250	135	1.0	2.2	calm	29
251	114	5.0	3.9	calm	29
265	82	3.3	1.6	calm	29
266	110	2.7	1.6	1	29
276	142	3.9	2.7	1	29
284	87	4.0	3.9	calm	29

Movements on the home range.—The daily movements on each home range followed a consistent pattern, especially on clear, cold days. The juncos in flock II emerged from the roosting trees when light intensity was between 1.1 and 4.3 luces. On overcast mornings, the birds left 12 to 18 (mean = 14) min before sunrise; on clear mornings 20 to 25 (mean = 23) min before sunrise. Temperature had no effect on the time of roost leaving (linear regression; $r = .2$).

Once out of the roost, the birds perched in nearby trees for variable lengths of time. The duration of this early morning perching activity was related to air temperature (Fig. 4). For example at –25°C, less than 10 min elapsed between roost leaving and first feeding, compared to 20 or more min elapsing at temperatures above 0°C.

After leaving the roost areas, the flocks followed a feeding circuit which took them .5 to 1 km away from the roosting areas, depending on the home range (58 observations). The farthest points from the roosting areas were used from mid-morning until late afternoon. Then the flocks started back toward the roosting areas, following a route similar to that used in the morning. On days with snow accumulation, high winds, or low temperatures, the movements away from and back to the roost were irregular, as many individuals left the flock for varying amounts of time.

There were 2 main types of early-morning feeding behavior. On home range I and IIB, the flocks gradually worked across a large field as they moved from the night roost, although there were some reverse movements. There were usually 11 or 12 moves per hour, but these moves were reduced to 4 to 6 per hour on windy days (winds over 32 kph), or on days with temperatures below –7°C ($t = 3.62$, $P < 0.01$, 12 df).

On home range IIA, the birds fed for approximately an hour in a short

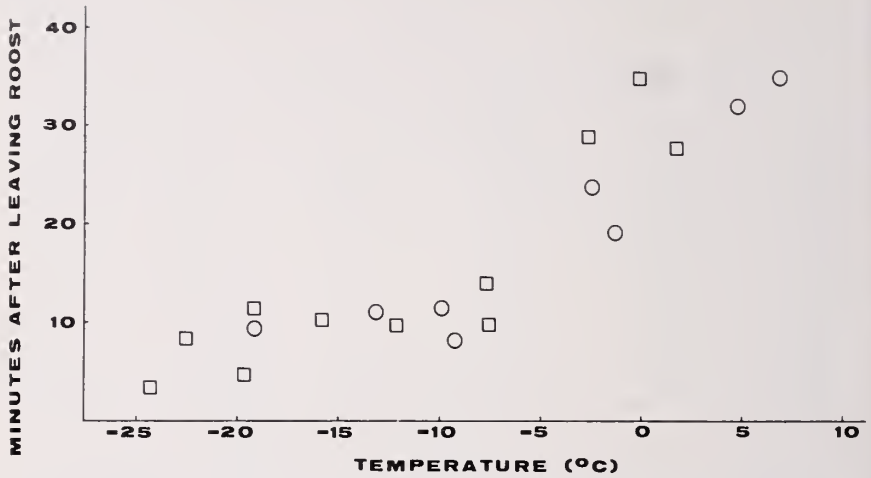


FIG. 4. Minutes elapsed between leaving roost tree and first visits to feeding areas as related to temperature. Squares indicate February observations, circles March observations ($r = 0.87$, $P < 0.01$).

grass pasture after leaving the roosting area each morning, then made a long flight to an area 600 m away where they remained for most of the day. Thirteen hectares of this flyway, which lacked tall vegetation were never used for feeding.

The only observable seasonal differences in feeding activities were in the portions of the cultivated fields that were used. During the fall migration, large flocks of juncos usually were widely dispersed in a harvested soybean field, often flying directly into its center. During mid-winter, the flock fed mostly near trees at the field edge, gradually moving toward the center of the field. In late winter and early spring, the birds began flying directly to the center of the field again, perhaps due to the depletion of the food supply near the edges (see West 1967).

Junco flocks merged temporarily at various times. Flock I merged with an adjacent junco flock each afternoon for about an hour (26 observations). This merging occurred in an area where the home ranges of the 2 flocks overlapped, and ended when one of the flocks flew out of the area. Flock II never merged with another flock, although one was sometimes only 100 m away.

DISCUSSION

Our findings on habitat use agree in most respects with those of other workers. However, some other published observations on junco habitat

use do not include cultivated fields (Quay 1947, Johns 1971), and only Graber and Graber (1963) and Pulliam and Enders (1971) noted as wide a range in habitat preference.

The change in home range area by flock II is somewhat perplexing. The flock could have "forgotten" the boundaries of the old home range after the long period of snow accumulation, but this seems an unlikely explanation. Whittle and Fletcher (1924) have documented that juncos may winter year after year in the same locality. If juncos can find their way back to a previous wintering area, they would surely remember home range boundaries after only one month. It is unlikely that the food supply was depleted in the first home range, as the flock used only a small percentage of the home range for feeding. The juncos may have changed home ranges because the long period of snow accumulation reduced their fat reserves sufficiently that they could no longer afford to waste energy just flying over large areas of the home range.

This last possibility may explain why home range IIB was half the size of home range IIA. In home range IIA (33 ha), only 2 ends were intensively used; much of the rest was merely flown over. In contrast, most of the 17 ha of home range IIB was used for feeding. The areas actually used for feeding in both home ranges are similar in size, thus indicating that the needs of a flock of 11 to 13 juncos could be supplied by about 16 ha.

According to West (1967) a flock of 10 to 20 Tree Sparrows (*Spizella arborea*) can find enough seeds in 1 ha to survive through the winter. Yet, both juncos and Tree Sparrows travel daily over relatively large areas (Helms and Drury 1960). Covering more area in the winter home range than is actually needed for a food supply may have 3 major functions. By being familiar with many potential feeding areas, the birds may, in times of food unavailability (after snow and ice storms), be more successful in finding food. In addition, an increase in area covered may reduce interactions among members of the flock, thus promoting flock stability. By constantly moving about, losses through predation may also be reduced. Crowcroft (1966) observed that mice (*Mus musculus*) exhibit this feeding strategy even when food is abundant.

Juncos fed on seeds that were on the ground except during periods of high snow accumulation when they were forced to feed on seeds still on plants. They either pulled the seed head to the ground, or perched on the plant while eating. West (1967) has shown that more than 90% of the annual seedfall in Illinois occurs by January. After the 30 January snow fall, the juncos of flock II were forced up onto the forbs, but if the seedfall was mostly complete, the juncos may have been feeding on the vegetative

parts of forbs or very sparse seeds. This poor diet may have been the reason why the junco groups left their feeding areas within the home range and gathered at the cattle pens in early February.

Our observations on the feeding heights of juncos are similar to those of Johns (1971) who found that 95% of the juncos' feeding activities occurred on the ground. However, Pulliam and Enders (1971) reported that juncos spent only 35% of their feeding time searching for food on the ground. The causes of these differences are not evident.

Wintering birds may metabolize up to 15% of their body weight during the night (Kendeigh 1934, Newton 1969), therefore the presence of protected winter roost sites that can minimize energy losses may be essential for birds to inhabit an area. An opaque cover reduces radiation heat loss and any wind-stopping material reduces convection heat loss (Moore 1945, Gates 1962). The wintering juncos in this study used well-protected sites. Most of them roosted in conifers. The juncos which roosted in tall grass or in brush piles were in areas without pines and in which cedars were so scattered that the flock would have been widely dispersed if each bird had roosted in an unoccupied tree. The inference is that conifers, where available, are selectively used for roosting in preference to tall grass or brush piles. During migration, when junco flocks are large and mobile, roosting in tall or fallen grass may be very common.

SUMMARY

The movements and habitat preference of 2 flocks of Dark-eyed Juncos were studied in the winter of 1971–1972. One flock established a new home range following a heavy snow fall. The 3 home ranges were found to be 27, 33, and 17 ha in area. Each flock night-roosted in dense vegetation at one end of the home range, and spent midday at the opposite end. Most feeding activities were restricted to areas containing grasses and forbs with taller vegetation in the general vicinity. Most day-light hours were spent in scrub and in short grass pasture habitats. Home range overlap of 2 junco flocks resulted in temporary intermingling among members of the flocks at certain times during the day.

ACKNOWLEDGMENTS

We are grateful to Drs. David Osborne and Charles Thompson for making critical comments on this paper. Harvey Kimble, Lee Rowland, and Calvin Spencer kindly allowed this study to be conducted on their land.

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DEPT. OF BIOLOGICAL SCIENCES, WESTERN ILLINOIS UNIV., MACOMB 61455. (PRESENT ADDRESS: BMG, DEPT. OF ZOOLOGY, MIAMI UNIV., OXFORD, OHIO 45056). ACCEPTED 15 JAN. 1975.

ADDITIONAL RECORDS OF PASSERINE TERRESTRIAL GAITS

George A. Clark, Jr.

The varied methods of locomotion in birds pose significant problems in behavior, ecology, adaptation, and evolution. On the ground birds progress with their legs moving either synchronously (hopping) or asynchronously (walking, running) as the extreme conditions. Relatively terrestrial species often have asynchronous gaits, whereas primarily arboreal species are typically synchronous on the ground. Particularly important earlier studies on passerines are Kunkel's (1962) comparative behavioral survey and Rüggeberg's (1960) analysis of the morphological correlates of gaits. Over several years I have noted gaits for 47 passerine species in the U.S., England, and Kenya, and have examined many references. I here summarize behavioral records for families not mentioned by Kunkel (1962) and also for species with gaits markedly unlike those of confamilial species discussed by him. My supplementary review is selective rather than exhaustive with the aim of indicating more fully the distribution of gaits among the passerine families. Regional handbooks, life history studies, and other publications contain numerous additional records, but I know of none that negate the conclusions presented here. J. S. Greenlaw (in prep.) has reviewed elsewhere the passerine double-scratch foraging behavior that has at times previously been discussed in connection with gaits (e.g., in Hailman 1973).

VARIATION WITHIN SPECIES

Gaits often vary within a species (Kunkel 1962, Hailman 1973, Schwartz 1964, Gobeil 1968, Eliot *in* Bent 1968:669-670, this study). As an additional example, I have seen Common Grackles (*Quiscalus quiscula*) hop in contrast to their usual walk. Such intraspecific variation is possibly related to both substrate and speed of locomotion (Hailman 1973), but further studies will be necessary to clarify the possible relationships.

Ontogenetic changes can result in intraspecific variation in gaits (Nice 1943, Kunkel 1962). Recent records are summarized in Table 1. Some species change little, if at all, ontogenetically as I have noted for the House Sparrow (*Passer domesticus*) in which both fledglings and adults hop. Another source of variation within species is difference between foraging and display gaits (see, for example, Delius 1969, Miller 1951, Rowley 1962, Schwartz 1964). Injuries or malformations also contribute to intraspecific

TABLE 1

EXAMPLES OF ONTOGENETIC CHANGES IN GAIT

Species	Juvenile gait	Adult gait	Reference
Gymnorhinus cyanocephalus	hop	walk	Ligon 1974
Mimus polyglottos	hop	walk	Horwich 1969
Cossypha natalensis	step and hop	hop	Farkas 1969
Oenanthe oenanthe	walk	hop	N. Smith in Ficken and Ficken 1966

variation. As examples, I have seen Starlings (*Sturnus vulgaris*), a Red-winged Blackbird (*Agelaius phoeniceus*), Common Grackle, and Dark-eyed Junco (*Junco hyemalis*) jump along on only one functioning leg: the first 3 of these typically walk. In addition, Nickell (1965) observed such jumping by a one-legged American Robin (*Turdus migratorius*). As Short (1971) noted, birds with a capability for asynchronous leg movements and a concomitant ability to balance on one leg appear more likely to survive if a leg is lost or injured than do birds that hop and cannot balance on one leg.

Observation and reporting of gaits can contribute artifactual variation. Details are not easily seen for rapid movements. Description is particularly difficult for gaits intermediate between walking and hopping as seen in the Philippine Glossy Starling (*Aplonis panayensis*, Restall 1969) and the African White-browed Sparrow Weaver (*Plocepasser mahali*, this study). Finally, caution should be used regarding published reports, for Harrison (1969) mentions that some authors have used "running" as a synonym for "moving rapidly" without implying an asynchronous gait.

VARIATION AMONG SPECIES

Despite variation within species and the lack of detail in many reports, existing data indicate major differences among certain taxa.

Furnariidae.—Walking or running apparently typify the Furnariinae (*Geositta, Upucerthia, Eremobius, Cinclodes, Furnarius*; Wetmore 1926, Feduccia 1970). In contrast, Buff-throated Foliage-gleaners (*Automolus ochrolaemus*) of the more arboreal Philydorinae hop over the ground (Skutch 1969a). In the Synallaxinae the Slaty Spinetail (*Synallaxis brachyura*, Skutch 1969a) and Rufous-fronted Thornbird (*Phacellodomus rufifrons*, Skutch 1969b) hop, but Wetmore (1926) reported walking or

running for canasteros (*Asthenes dorbignyi, A. patagonica*) and Lark-like Brush-runners (*Coryphistera alaudina*). Sharp-tailed Streamcreepers (*Lochmias nematura*) of the subfamily Sclerurinae walk (Mitchell 1957), whereas leafscrapers (*Sclerurus*) hop (Skutch 1969a) or run (Slud 1964).

Formicariidae.—Members of this family hop except for the walking of the terrestrial antthrushes (*Formicarius*; Skutch 1969a, Slud 1964, Wetmore 1926, Willis 1967, 1969).

Cotingidae.—I have seen a caged Andean Cock-of-the-rock (*Rupicola peruviana*) hopping.

Pipridae.—Skutch (1969a) reported a Blue-crowned Manakin (*Pipra coronata*) hopping on boards off the ground.

Tyrannidae.—Asynchronous gaits occur commonly in the genera *Corythopis, Agriornis, Xolmis, Muscisaxicola, Lessonia, Muscigralla, Myiotheretes, Hymenops, Fluvicola, Machetornis,* and *Serpophaga* (Haverschmidt 1968, Wetmore 1926, Short and Morony 1969, Hudson 1920, Smith 1971a, b). At least Negrito Flycatchers (*Lessonia rufa*, Wetmore 1926) and ground tyrants (*Muscisaxicola*, Smith 1971a) both hop and run. More arboreal flycatchers such as kingbirds (*Tyrannus* spp., Youngworth 1937) and Vermillion-crowned Flycatchers (*Myiozetetes similis*, Skutch 1960) hop occasionally when on the ground.

Dicruridae.—I have seen the African drongo *Dicrurus adsimilis* hop.

Corvidae.—Kunkel (1962) did not mention the walking characteristic of the adult Piñon Jay (*Gymnorhinus cyanocephalus*, Ligon 1974).

Cracticidae.—Within this heterogeneous family the walking of the Australian Magpie (*Gymnorhina tibicen*, Kramer cited in Kunkel 1962) contrasts with the hopping of the Pied Currawong (*Strepera graculina*, Frith 1969).

Grallinidae.—Torrent Larks (*Grallina bruijni*) walk (Diamond 1972) unlike the hopping of Apostlebirds (*Struthidea cinerea*, Austin 1967).

Timaliidae.—In the subfamily Orthonychinae, Spine-tailed Logrunners (*Orthonyx temminckii*) and 2 species of Scrub-robins (*Ptilorrhoa*) have asynchronous gaits (Rand and Gilliard 1968, Diamond 1972), whereas Lesser Melampittas (*Melampitta lugubris*) hop (Rand and Gilliard 1968).

Numerous species of the subfamily Timaliinae hop (Kunkel 1962), but Black-capped Babblers (*Pellorneum capistratum*, Smythies 1968) and Gray-crowned Babblers (*Pomatostomus temporalis*, Frith 1969) have asynchronous gaits.

Campephagidae.—Ali and Ripley (1971) report hopping by Black-headed Cuckoo-shrikes (*Coracina melanoptera*). In contrast, Ground Cuckoo-shrikes (*Pteropodocys maxima*) run (Serventy and Whittell 1962).

Muscicapidae.—The running gait of Silverbirds (*Empidornis semipartitus*, Mackworth-Praed and Grant 1960) is apparently unusual for this family.

Laniidae.—Unlike other shrikes, Bush-shrikes (*Tchagra*) run over the ground (G. G. Olivier in Thomson 1964:735).

Parulidae.—Kunkel (1962) cited the typically asynchronous gaits of *Seiurus* (cf. Schwartz 1964), but probably many New World warblers hop when on the ground, as seen by me for the Yellow-rumped Warbler (*Dendroica coronata*) and by Ficken (1962) for redstarts (*Setophaga ruticilla*).

Icteridae.—Contrary to Kunkel (1962), orioles (*Icterus*) probably typically hop when on the ground as both Youngworth (1937) and I have observed for the Northern Oriole (*I. g. galbula*).

DISCUSSION

Kunkel (1962) reported conspicuous differences in gait (predominantly synchronous versus mainly asynchronous) between species within the Corvidae, Turdidae, Sylviidae, Sturnidae, Ploceidae, Icteridae, Carduelinae, and Emberizinae. From my review 11 other families or subfamilies may be added to his list: Furnariidae, Formicariidae, Tyrannidae, Cracticidae, Grallinidae, Orthonychinae, Timaliinae, Campephagidae, Muscicapidae, Laniidae, and Parulidae. Thus at least 19 higher taxa of passerines reportedly contain both species with chiefly asynchronous gaits and species that are mainly synchronous. The presence of 2 alternative species-specific phenotypes in each of these higher taxa indicates considerable evolutionary convergence in gaits (Clark 1973).

I know of no simple measurements that will enable predictions of gait from structure alone. Species with similar gaits but belonging to different families sometimes differ considerably in structure of the pelvic appendage, e.g., in relative leg length or limb proportions (Rüggeberg 1960).

Marked variation in terrestrial gaits within a species and within individuals raises the possibility that differences in gaits among species might not be due to inherited specifications for behavior per se. However, the structural differences associated with species differences in gaits (Rüggeberg 1960) are likely to be inherited and could influence the relative frequency of gaits. An analogous situation occurs in foraging in which inherited structure can facilitate eating certain foods, but birds, being behaviorally somewhat flexible, often can use unusual foods.

SUMMARY

Extremes in avian terrestrial gaits are hopping (synchronous leg movements) as opposed to walking or running (asynchronous). This review summarizes newer records for gaits of passerine families and subfamilies. At least 19 of these higher taxa include both species that are largely synchronous and species that are chiefly asynchronous. Variation within many species indicates that gait behavior per se might not be directly inherited. Presumably inherited structural differences between species contribute to the ontogenetic development of taxonomic differences in gait.

ACKNOWLEDGMENTS

I thank F. Enders, J. S. Greenlaw, J. P. Hailman, and J. A. Slater for helpful comments and suggestions.

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Biological Sciences Group, Univ. of Connecticut, Storrs 06268. Accepted 3 Jan. 1975.

CHANGES IN BODY WEIGHT OF AMERICAN GOLDFINCHES

Arthur J. Wiseman

Various authors (e.g., Baldwin and Kendeigh 1938:416; Fisher 1955:59; Perrins 1964:883) have commented that body weights of wild species of birds have not received adequate attention. Though seldom published, vast amounts of weight data have been collected in typical banding projects. As a result of my activities, I have accumulated weight and measurement data from banding 1567 American Goldfinches (*Spinus tristis*). To make these available, I present here an analysis of seasonal and sexual variation in body weight and simple comparisons of wing chord and body weight.

METHODS

These data were taken from a general banding program conducted for 5 years at the Cincinnati Nature Center, 25 km east of Cincinnati, Ohio. All birds were taken nonselectively by traps and nets. No birds were held captive or collected, and no experiments were done, so the bias created by trapping was thus held to a minimum. While not of prime interest at the time of banding, the goldfinches constituted over 15% of the bandings at the Nature Center.

Birds were captured on Sundays and Mondays throughout the year except the last half of December, from March 1967 through July 1972. Each day, unless it was raining, the traps were opened at dawn and operated as long as birds were being captured. As a rule, on Sunday large numbers were trapped in the morning, then fewer in the afternoon, partially because of the banding activities. The morning of the second day was less fruitful and the afternoon captures were practically nil. The traps were used as feeding stations daily throughout the year, baited with sunflower seeds and grain mixtures or chicken scratch feed. Traps were operated at all seasons of the year; nets were used irregularly and only when the traps were not effectively attracting birds, particularly in warmer weather and when natural foods were abundant.

Six McCamey Chickadee traps, set 2 per tray on 3 elevated trays; one 6-cell Potter trap on the ground; and one 1 m × 2 m × 0.6 m all-purpose or figure-eight trap were used. These were placed within 20 m of and visible from a central permanent banding office. When needed, from one to seven 12 m, 30 mm mesh nets were set in an adjoining field planted with wildlife crops such as millet, sorghum, corn, sunflower, etc., and perennial plants yielding fruit or berries.

The time a bird was in captivity was held to a minimum. Generally, birds were collected at intervals of 10 to 15 min, placed into isolated chambers of a darkened box, and immediately taken to the office and processed. If a particularly large number of birds was captured, all traps and nets were closed until all captured birds were released. Birds were seldom in captivity for as long as 30 min.

Standard procedures in the office were to remove a bird from a box; determine the species, sex, and age; affix a U.S. Fish and Wildlife Service band; measure the wing chord and tail; determine the fat class; check for molt, breeding condition, abnormalities, injuries, etc.; and finally weigh and release the bird. The birds were

weighed to the nearest 0.1 g in an upright paper cone on an Ohaus triple-beam balance. The balance was occasionally checked for accuracy using standardized weights. I did all the processing, so no variations have resulted from different operators. My wife helped to remove birds from traps and nets, recorded all field information, transferred data to the individual bird's record card, and made these cards available at subsequent recaptures.

Sex of goldfinches was determined by plumage characteristics. Winter males were determined by their glossy black remiges and rectrices; on winter females these feathers were dull to brownish black. A few intermediates, usually young birds, were recorded as sex unknown and were excluded from the study unless later recapture established the sex.

Age was recorded and is presented here in the terminology of the U.S. Fish and Wildlife Service Bird Banding Laboratory as follows: HY (Hatching Year) = from hatching to the end of their first calendar year; SY (Second Year) = birds in their entire second calendar year; AHY (After Hatching Year) = a catchall class but for male goldfinches may be considered as after second year birds.

Age was determined by the following characteristics (see Olyphant 1972, Forbush 1929): *HY males.*—Skull pneumatization is not completed until end of year. Plumage is fresh in August–September. Juvenal lesser wing coverts are olive greenish-yellow; juvenal wingbars are buffy, fading to off-white, are narrow and become worn during second year. Fall molt replaces only head and body plumage. *SY males.*—Skull is fully pneumatized. Plumage is worn in August–September. Juvenal lesser wing coverts are as above. Juvenal wingbars are badly worn or absent. Fall molt is complete and lesser wing coverts and wingbars of an AHY male are attained in October–November of second year. See discussion below. *AHY males.*—Like SY males except lesser wing coverts are bright yellow and wingbars are broad and white. *HY females.*—Skull pneumatization is not completed until end of year. No standards were known to distinguish them after pneumatization is completed. *AHY females.*—Skull is fully pneumatized, see above.

I believe these characteristics permitted approximately 90% of the males to be aged correctly, but a few individuals are known to have failed to develop the bright yellow coverts even after reaching their third calendar year. A method of aging females published by Olyphant (1972) had been attempted, but some variations were noted so the procedure was abandoned before checking thoroughly.

Measurements were made of the unflattened chord from the bend of the wing to the tip of the longest primary with a rule under the folded wing (Wiseman 1970). The longest rectrix was measured by inserting a plastic rule between the central pair of rectrices, against the base of the tail.

Fat stores were subjectively recorded as fat classes 0–3: fat class 0 = none to trace amounts; fat class 1 = moderate amounts in the furculum, but not sufficient on the abdomen to fully conceal the externally observable viscera; class 2 = furculum filled to level with the clavicles, the abdomen with a layer concealing the viscera; class 3 = furculum bulging convexly, the abdomen distended with a layer of fat.

Weather data were taken from official reports of the U.S. Weather Bureau station at Greater Cincinnati Airport, about 30 km WSW of the Nature Center.

Calculations.—Basic statistics of these data were calculated using an IBM 765/360 computer at the University of Cincinnati. Because of the many small samples involved, "N-1" was substituted for "N" in the formulae for calculating both the stan-

dard deviation (S.D.) and the standard error of the mean (S.E.), and these formulae were used throughout the study. Means ± 2 S.E. were used to measure probability at the 95% level. Regardless of how meager a sample was, it was plotted into the charts if ± 2 S.E. remained within the range of the sample.

If a bird was captured more than once on the same day, only the initial capture data were used for that day. When birds were taken on consecutive days, both weights were included in the study (see discussion below). One bird, an HY male weighing 9.3 g in October, was so far below the other male weights it was considered abnormal and was excluded. Any birds found to have missing or broken remiges and/or rectrices, and all birds molting these feathers in the fall were excluded from analysis of wing and tail measurements. The effects of netting versus trapping of birds was considered negligible, so these groups were pooled. Throughout the analysis, the sexes were treated as distinct populations.

For anyone wishing more details, the data have been keypunched and are available on request.

RESULTS AND DISCUSSION

Capture rates and samples.—The numbers of male goldfinches captured were always larger than the numbers of females (no field observations were made of the sex ratio). The aggressive nature of the males may have contributed slightly to their higher capture rate.

Table 1 lists the dates (by month) of 1448 captures of 978 individual males and 756 captures of 538 females. Of these, 726 males were captured only once, 148 were captured twice, 56 were taken 3 times, and 47 males were taken 4 to 10 times. One male (#107–31428) provided 19 useful weights from 1968 until last seen on 5 April 1971. Of the females, 413 were captured once, 78 twice, 25 three times, and 21 were taken 4 to 6 times. One female (#116–37283) provided 12 adult weights between 1 September 1969 and 9 April 1972.

Generally, from January through April the goldfinches were trapped, whereas in the remainder of the year they were netted. At the start of the program, very few were trapped. Beginning in February 1970, for unknown reasons, large numbers of goldfinches came and were trapped in both ground level and elevated traps. They disappeared from our trapping area at the end of April, about the time natural foods became abundant. The number of goldfinches netted was influenced by a variety of conditions, including: rate of growth and yield of food crops, sufficient height of plants to conceal the nets, and the abundance of all birds in the field. At times, all nets had to be closed in order to process the large number of netted birds and, occasionally, some birds were released without processing.

On some mornings as many as 125 to 150 birds were processed during the first 5 or 6 hours. In these instances, birds that had been previously

TABLE 1

DISTRIBUTION OF CAPTURES BY MONTHS AND YEARS FOR 978 MALE AND 538 FEMALE GOLDFINCHES

MONTH		1967	1968	1969	1970	1971	1972	Totals
JAN	M	N*	0	0	3	35	33	71
	F	N	0	0	0	15	12	27
FEB	M	N	0	0	151	N	44	195
	F	N	0	0	64	N	28	92
MAR	M	0**	0	2	160	26**	97	285
	F	0**	0	1	85	12**	54	152
APR	M	1	0	0	68	266	103	438
	F	1	0	0	39	106	48	194
MAY	M	9	0	8	0	11	4	32
	F	7	0	3	0	8	8	26
JUN	M	27	3	5	2	1	0	38
	F	9	3	8	0	1	0	21
JUL	M	5	4	30	1	11	N	51
	F	6	2	21	5	2	N	36
AUG	M	3	48	41	18	5	N	115
	F	2	29	10	3	1	N	45
SEP	M	19	68	16	31	2	N	136
	F	23	43	12	31	1	N	110
OCT	M	53	0	6	6	0	N	65
	F	35	1	4	4	0	N	44
NOV	M	5	2	11	2	0	N	20
	F	0	0	6	0	0	N	6
DEC**	M	0	0	0	2	0	N	2
	F	0	0	0	3	0	N	3
TOTALS	M	122	125	119	444	357	281	1448
	F	83	78	65	234	146	150	756

* N = not operating; ** = partial operation with number of captures for shortened period.

banded were merely examined and weighed, resulting in incomplete measurement records.

Migration.—I found no evidence of migration either by a pre-migratory build-up of fat or by recoveries of birds elsewhere. Over a dozen individuals, including both sexes, were captured in both summer and winter, indicating that some birds may be residents.

Monthly weight variations.—Each sex shows an inverse correlation of weight with ambient temperature (Fig. 1) as has been shown with other species (e.g., Baldwin and Kendeigh 1938, Odum 1949, Helms and Drury

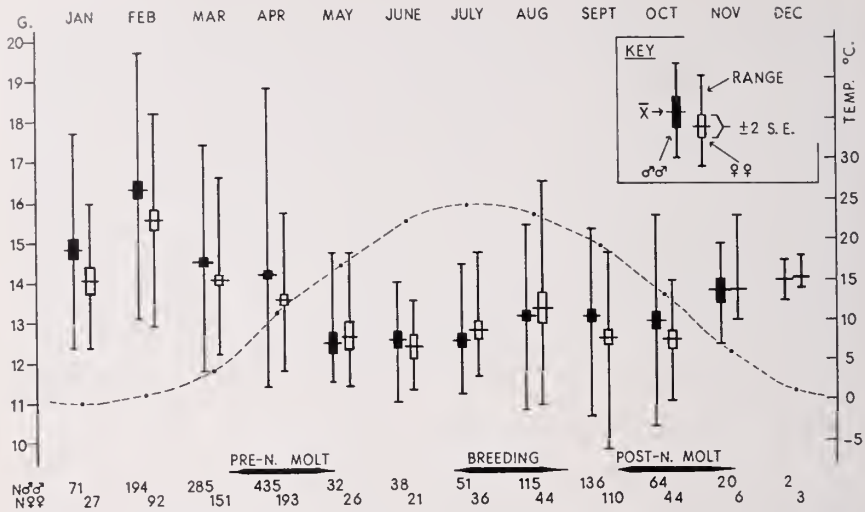

FIG. 1. Annual cycle of body weights of American Goldfinches, all years and all age groups of each sex combined. N = sample size. Ambient temperatures are monthly means (dots) connected by dashed line.

1960). The lowest temperatures (mean 0°C) were in January, but the mean body weight of each sex peaked in February (mean temperature 1°C), a lag similar to that noted by Odum (1949). By March the temperature had risen (mean 4°C) and the mean body weight had started to drop. This drop continued into summer, but in both sexes the rate of drop was much less from March to April than from April to May. This difference in rate of weight decrease may be related to the molt in April. King et al. (1965:244) found an increase in non-fat body weight correlated with the molts of White-crowned Sparrows (*Zonotrichia leucophrys*) and suggested that, "Although the components of this variation have not been investigated, it seems probable that follicular enlargement, growth of papillae, and variations in blood volume must contribute the major fractions."

Through the winter, female goldfinches averaged about 0.5 to 0.9 g lighter than the males, but May females were about 0.2 g heavier. The female begins and ends the prenuptial molt about 10 days later than does the male. Although the males had completed the molt in April, the females were still molting in early May and had a heavier mean body weight. In June, females were again lighter than males and both were at their lowest mean weights of the year.

In July, as temperature peaked (mean 25°C), female goldfinches showed an increase in mean weight not found in males. My field notes as well as

Mundinger (1972) indicate the incubation patch was developing at that time. In August, both sexes reached their maximum mean weight of the summer. King et al. (1965) found that in female White-crowned Sparrows the maximum body weight in summer accompanied the period of maximum oogensis. The goldfinch nests in August locally, and the increase in weight in both sexes seems correlated with breeding.

In September, males remained at a high mean weight, whereas females dropped in weight. King et al. (1965) reported a similar drop in weight in White-crowned Sparrows which they related with either the greater attentiveness to the young by the female, the partial involution of the reproductive organs, or possibly a combination of these. The newly fledged young are included in the September samples along with the adults who were caring for them. The effects on the mean weights exerted by the young will be detailed later.

By October most adults had dispersed, becoming secretive during their postnuptial molt. The young, on their own while undergoing their partial (body feathers only) postjuvenal molt, remained in loose flocks and were captured in fair numbers. When compared with the September mean weights (see Fig. 4) for respective age groups, the October samples showed 58 HY males lost an average of 0.1 g, 35 HY females gained 0.2 g, 6 AHY males gained over 1 g, and 9 AHY females lost about 0.6 g. Relatively more males than females were in molt in October. Though not statistically significant, these changes suggest that more work and larger samples at this period of the year would confirm the trend.

The November and December samples, though small, tend to indicate a gradual increase in weight toward the higher winter levels. In November, the females (5 HY and 1 AHY) were all in molt, whereas 8 of the males were AHY birds and some of these had completed their molt.

Variations in wing chord and tail measurements.—Mean female wing and tail measurements (Fig. 2) in all months were significantly shorter (about 2.5 to 3.0 mm on the wing chord and about 1.4 to 2.0 mm on the tail) than the mean measurements of males, but the ranges of measurements of the sexes overlapped considerably throughout the year. Changes in feather length, obviously due to wear, continued throughout the year until the fall molt. The degree of wing and tail wear was about the same for the sexes, but was more severe on the tail. The combined November and December samples indicate the increase expected after the adult molt. The variation in size and age, as well as wing chord to weight relationship, will be detailed later.

Basic mean body weight and rate of increase.—For later comparisons, I decided to determine the basic mean body weight for each sex: the

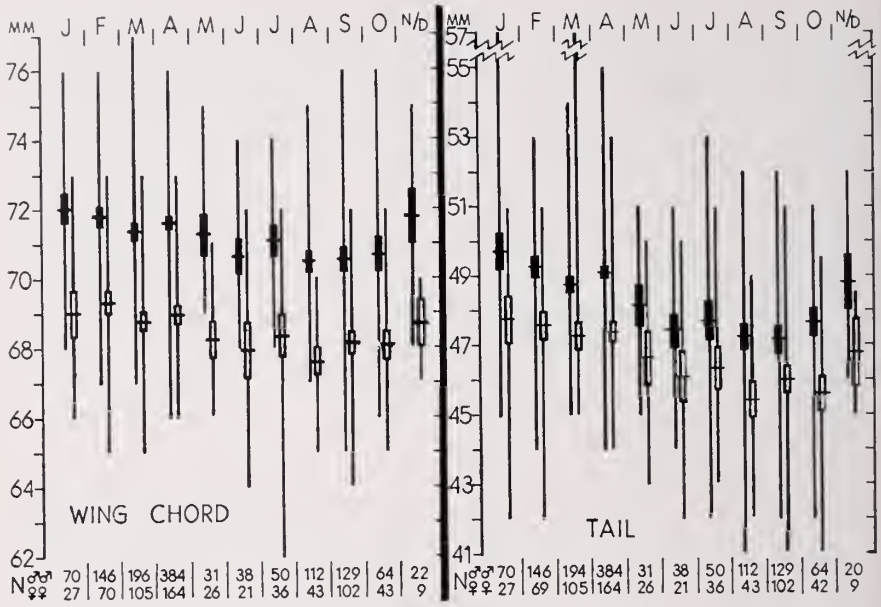

FIG. 2. Annual cycle of wing chord and tail measurements. All years and all age groups of each sex combined. Conventions as in Fig. 1.

lowest weight of the year when the body contained a minimum of fat. I also wanted to know the hourly rate and/or percentage of increase in weight occuring in one day when the weight was at this basic level. The basic weights included the food present in the body, of course, because food is a vital part of the hourly and daily variations in weight which occur naturally in all animals. I was not determining a "fat-free" weight as have others (e.g., Connell et al. 1960, King et al. 1965, Odum et al. 1961) who extracted the total lipids from a dead body by chemical means; my birds were alive and active

In June, both sexes were at their lowest mean weights, but the samples were too small to permit the computation of an hourly rate of change. Noting the males in May, June, and July had essentially the same mean weights, range, and S.E., I combined these months to form a sample of 121 males with a mean weight of 12.5 g. When the age groups were tested, the variation was only 0.1 g. The combined sample was then separated by hours and a mean weight calculated for each hourly period (Fig. 3). A linear regression computed from the hourly means showed an increase of slightly less than 0.05 g per hour for an increase of about 4% for the day. When the same procedure was applied to the female weights for

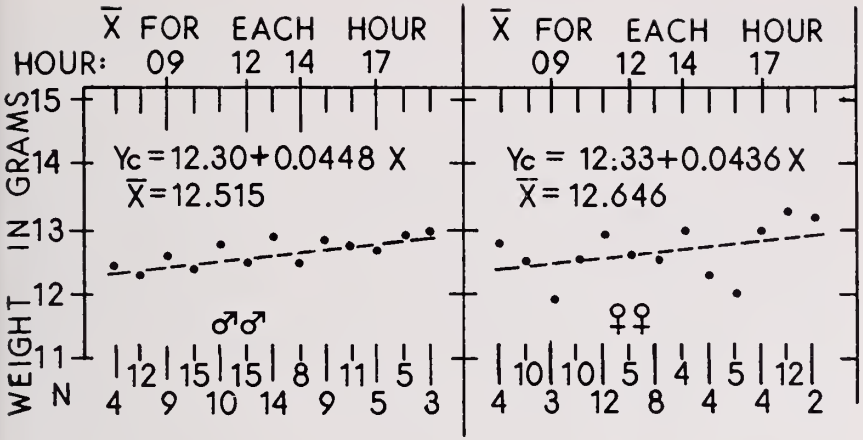

FIG. 3. Means of diurnal weights (dots) by hour of capture during May–July (data pooled) with regression line calculated from means. Conventions as in Fig. 1.

those 3 months, the combined sample indicated the females were the heavier sex which is not true for most of the year. Therefore, the mean weight was discarded; instead I used the June mean weight of 12.4 g. The linear regression showed a rate of increase essentially the same as for males, and as this seemed normal, it was retained. The reason the mean weight of females, as determined in Fig. 3 is high, is due at least in part to molt of females in May as discussed above and the start of gonadal activity in July, which will be discussed later.

Finally, after preliminary testing of these figures, I used basic mean weights of 12.5 g for males and 12.4 g for females and 4% as the rate of increase for one day for both sexes in comparisons with other periods.

Variations in weight during the breeding season.—During July, the incubation patch was developing and the mean weight of females increased 3.3% above the basic (June) mean weight. In August, most females had a well formed, vascular incubation patch and some occasionally showed abdominal distention which I associated with a mature egg about to be laid. Holcomb (1969) reported a mean date for clutch completion of late July for goldfinches in northern Ohio. While I have not recorded nest dates, breeding conditions observed on banded females indicated eggs were laid in late July and in August. Two females (#107–31198 and 31200) were taken on 18 August 1968 at 18:45 weighing 16.5 g and 16.1 g; as their abdomens were swollen, it seemed they were ready to lay eggs. A third female (#107–31201) was taken the same day at 19:30 weighing only 13.2 g; as she had a good brood patch, I concluded she had com-

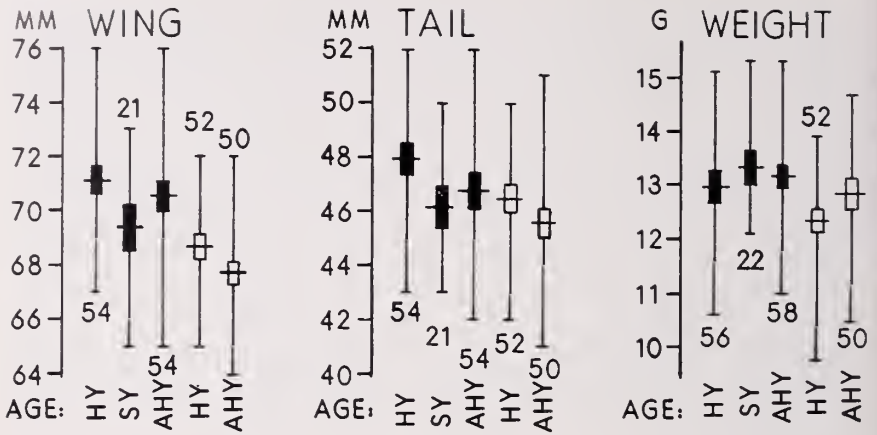

Fig. 4. Wing chord, tail measurements, and weights of individual age groups from September, all years combined. Conventions as in Fig. 1.

pleted her clutch. The heavier females were up to 33% above the basic mean weight, and the total August sample of females (13.3 g) was 7.3% above the June mean. One female, banded as an HY in September 1967 weighing 12.4 g. was taken 25 August 1968 weighing 15.6 g. an increase of 26% over the juvenal weight.

In contrast, in July the males showed only slight indications of being in breeding condition and no increase in weight. In August, individual males showed varying degrees of cloacal protuberance and while the mean weight increased to 13.1 g, this was only 4.9% above the basic mean.

King et al. (1965:238) found in White-crowned Sparrows that the lipid index in females, though not statistically significant, was greater than that of the males during the breeding season. They attributed this, at least in part, to the lipid content of the ova which were included in the extractions. Morton et al. (1973:85) found in female White-crowneds that "visible" fat stores were maintained through incubation. In my fat index scheme, small or trace amounts of fat were not recorded, but as all breeding females were noted as fat 0 (except one in class 1), the visible fat deposits must have been minimal. Apparently, most of the gain in weight in female goldfinches was from enlargement of the gonads and eggs and an accompanying increase in internal lipids, as suggested by King et al. (1965).

Influence of age on mean weights and measurements.—In September, the newly fledged young in fresh plumage became an important factor in the samples; the adults (including SY birds), not yet molted, were attending

them. In Fig. 4, the measurements and weights from September are presented for the various age and sex groups. The HY birds showed a significantly longer mean wing chord than the SY males and the adult females, which influenced the results in Fig. 2. A less important, but nearly identical relation existed in the tail measurements. In the weights, however, only the HY females had a significantly lower mean weight than the other groups.

In considering the ratio of wing chord to weight, the HY males had a longer wing but lower weight than the SY males which had the shortest wing but heaviest weight of males. In females, the HY birds had a longer wing but a lower weight than the adults, but both ages showed mean wing chords well below the means of most of the male groups. It is apparent that age, sex, and feather conditions are variables influencing the size/weight ratio of a bird.

Effects of date and hour of capture on mean weights.—Panel A in Fig. 5 compares the weights of both sexes on individual weekends of February and March 1970. On 15–16 February, a layer of ice covered the landscape, temperatures were below normal, and an exceptionally high number of birds was captured. Also, the 1970 weights peaked: the mean weight of males (17.0 g) was 35.6% above the basic mean while the female mean weight (16.6 g) was 34.4% above their basic mean. Although the first 3 weekends showed mean weights above the February mean in Fig. 1, the final weekend showed a statistically significant drop in weight in both sexes. In March, as temperature began to rise, the mean weights tended to drop but with some adjustments for immediate weather conditions which will be detailed later. There were significant changes, upward and downward, in mean weights of both sexes. The date of capture had an effect on the total sample.

In Panel B of Fig. 5, the male captures were divided into hourly periods and mean weights calculated for these. In February 1970, the earlier means were significantly lower than those of the late hours and the importance of the hour of capture is clear. In March, however, the only significant difference noted was between 07:00 and 11:00, but the highest hourly mean weight for March, recorded at 11:00, was significantly lower than many of the February hourly means. Then, when the first mean of the day (14.9 g) was compared with the last mean (17.7 g), February weights showed an increase of 18.8%. However, in March, these weights (14.2, 15.0 g) indicated the gain was only 5.6%. As the weights in March did not tend to increase throughout the day and a smaller percentage increase was recorded, it seems possible this is a clue to the system by which weight is lost in the late winter. Also, the hourly sample sizes in-

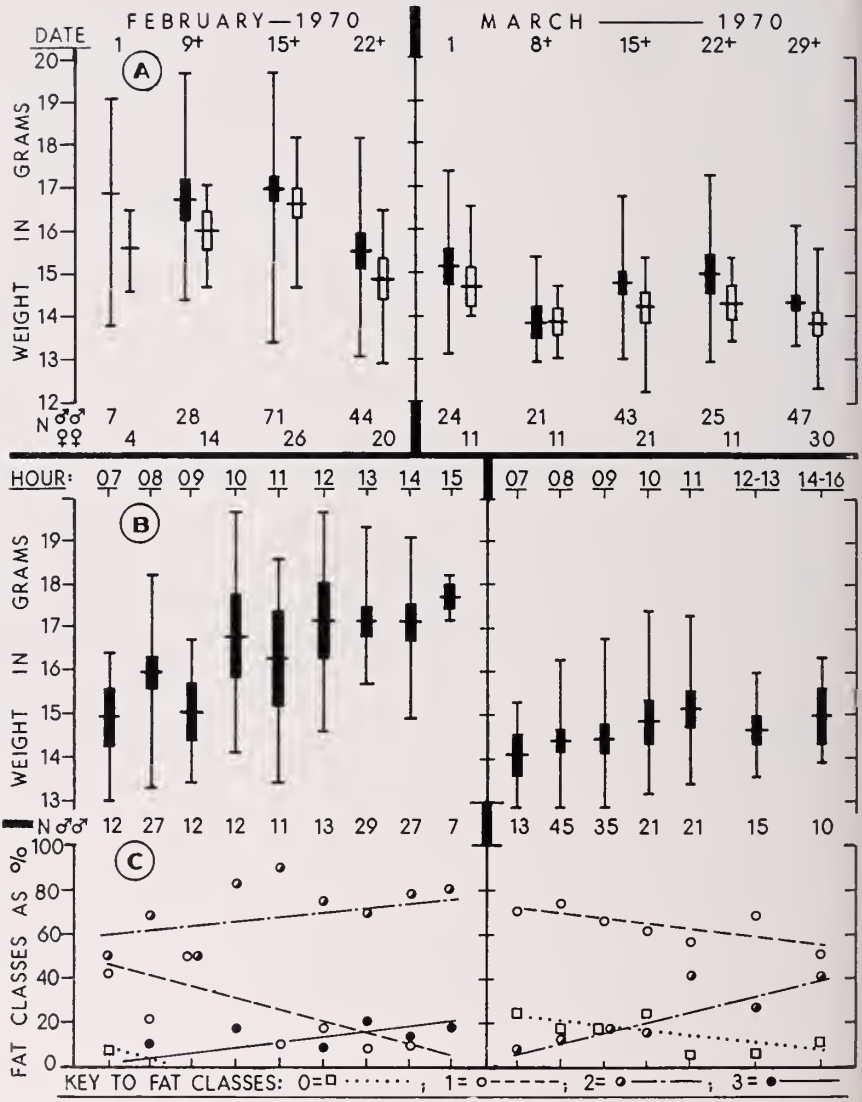

FIG. 5. Weights of samples from February and March 1970. A: samples from individual weekends, "+" following date indicates two days combined. B: samples of males only, weights from each month arranged by hour of capture. C: fat classes as a percentage of total sample for that hour and regression line calculated from percentages for each fat class. Conventions as in Fig. 1.

dicated high feeding activity extended into the afternoons in February, but less so in March. Similar comparisons of female weights indicate similar patterns would have resulted.

The following example demonstrates just how important the hour of capture can be when samples are compared. When I tested January samples, 34 males from 1971 had a mean weight of 14.5 g (S.E. = 0.16) while 33 males from 1972 had a mean of 15.2 g (S.E. = 0.16). Although significant, this difference was related directly to the hour of capture: over half the 1971 birds were taken before 10:00, but only one was taken this early in 1972. Odum (1949) eliminated the weights of birds captured before 10:00 to minimize the "daily rhythm factor," and thus made weights of banded birds comparable with those of collected birds taken only after noon.

The relation of hourly mean body weights to visible fat deposits.— Connell et al. (1960), King et al. (1965), and others found that increases in body weight can be directly attributed to increases in lipids in the body. Mueller and Berger (1966) and West and Peyton (1972) showed that higher weights were correlated with increases in visible fat deposits (classes). I tested to see if there was a relationship between the hourly mean weights and fat classes. In Panel C of Fig. 5, using the samples from Panel B, those males representing each fat class were converted to and charted as a percentage of the total hourly sample. For example: in February at 07:00 there were: 1 bird (8%) in class 0, 5 birds (42%) in class 1, 6 birds (50%) in class 2, but none in class 3. From the percentages a simple linear regression was computed. In February, class 1 birds were a high percentage of the sample in earlier hours, but diminished later in the day. Class 2 birds were a high percentage throughout the day, but the regression line indicated a gradual increase. Similarly, class 3 birds gradually increased throughout the day, but were a small fraction (20%) of the samples even at the highest point. Therefore, as the hourly weight increased, diurnal fat deposits were added and fat classes moved upward to higher classes related to the hourly mean weight.

In March, hourly mean weights and fat classes were lower. Only one bird was class 0 in February, but in March this group was a notable percent of the sample, but gradually decreased through the day. Class 1 birds also diminished in percentage, but were over 50% of the samples throughout the day. While class 2 birds increased in percentage, they were not the major fraction they were in February and class 3 birds were not recorded in March. (Of all my records of fat classes, class 3 was recorded regularly in February only and rarely in January or March.) The net results were consistent with the February findings, even though the fat

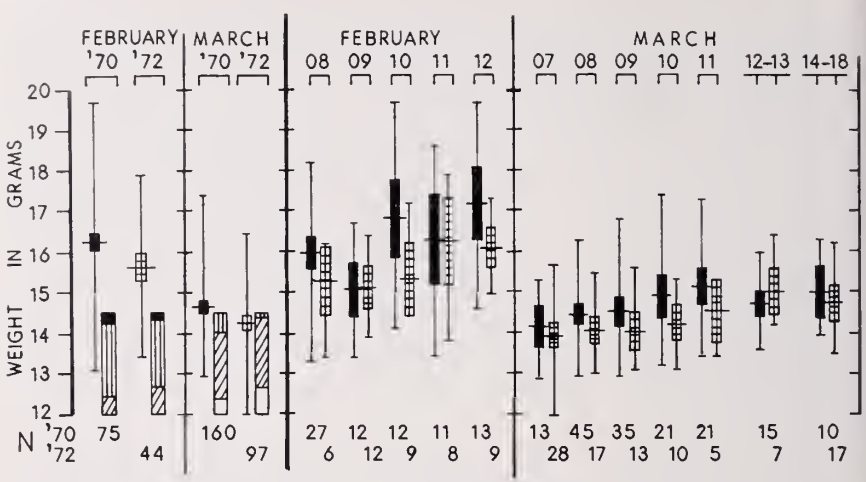

FIG. 6. Comparison of male weights from February and March of 1970 and 1972. First 2 panels present weights from samples for the months from each year and fat classes as percentage of the sample. Conventions as in Fig. 1, but filled rectangles are males from 1970 while cross-hatched rectangles are males from 1972. Key to fat classes: open rectangles = fat class 0; diagonal hatching = class 1; vertical hatching = class 2: filled rectangles = class 3. Last 2 panels present weights of males by hour of capture during month as listed at top.

classes were lower. Progressively into summer, fat classes continued to decrease. I detected no evidence of pre-migratory fat buildup.

Effects of handling on weights.—Various studies produced different results on this subject. While Mueller and Berger (1966) found a slight decrease in weight for birds recaptured on the same day, Helms and Drury (1960) found that these birds followed the normal diurnal trend of variation when averaged. When I examined my records, I found that most birds recaptured within 1 to 3 hours showed small weight losses, but after 6 to 8 hours these and other birds showed gains of 1 to 9%. However, because none of the birds recaptured in February or March had gained weight in line with the averages shown in Figure 5-B, I excluded all but the weights from initial captures for the day.

When I examined the records of birds captured on 2 consecutive days and considered the hours of capture, I found no consistent pattern. However, as these captures represented only about 1% of the weights and were scattered throughout the year, they were included.

Variation between years.—A study of male weights from February and March of both 1970 and 1972 was undertaken. However, in February 1972, the birds were taken only from 08:00 through 12:00, so it was

necessary to extract the birds captured in these hours in February 1970. In Fig. 6, the first panel compares the samples of males from these hours of February and the males from all hours of March for these years. In both months, the 1970 mean weights were significantly higher than the 1972 means.

In the same panel, the percentages of birds in the fat classes within each sample are charted. In February, the percentage of class 3 birds was greater while class 1 birds was smaller in 1970 than in 1972. Similarly, in March, the percentage of class 2 was greater while class 0 was smaller in 1970 than in 1972.

In the 2 final panels of Fig. 6, the weights of comparable hourly samples were studied. In February, the 1972 samples showed no significant changes, but in 1970 both the 10:00 and 12:00 samples were significantly above the 09:00 weights. Although not significant, the 3 even-numbered hours showed noticeably higher means in 1970 than in 1972. When I examined the male weights as weekend samples (not shown), the February 1972 peak mean weight (15.9 g) was reached on the first weekend, compared with 17.0 g on the third weekend of 1970 (see Fig. 5). Birds captured on the last 3 weekends of 1972 had mean weights below the lowest mean of the 1970 weekends. Weather conditions were not appreciably different in these years, so no explanation for these variations can be offered.

In March, the 1970 weights peaked at 11:00 (Fig. 6). While this was significantly above only the 07:00 weights of 1970, it was significantly higher than the 1972 hours of 07:00, 08:00, and 09:00. Again, no explanation can be offered. Smaller samples indicated similar trends for females in each period.

When April samples of males from 1970, 1971, and 1972 were compared (Fig. 7), no significant differences among the years were found. However, weekend samples from each year showed a variation in pattern. Consistent with the monthly trend in Fig. 1, a gradual downward slope in mean weights occurred in 1970 and 1971. However, in 1972 the birds were captured throughout the day only on 9 and 23 April. For unknown reasons, 60% of the birds were taken before 10:00 on 3 April, yielding an abnormally low mean weight. The mean was high and the sample small on 18 April as we did not work that morning. The need for comparing similar hours of capture (and banding efforts) is obvious.

The females from 1971 weekends were significantly lighter in weight than the males. Both sexes showed significantly higher mean weights on the first weekend and significantly lower means on the last weekend. Other female samples were too small for analysis. The exact effect of the prenuptial molt was not determined.

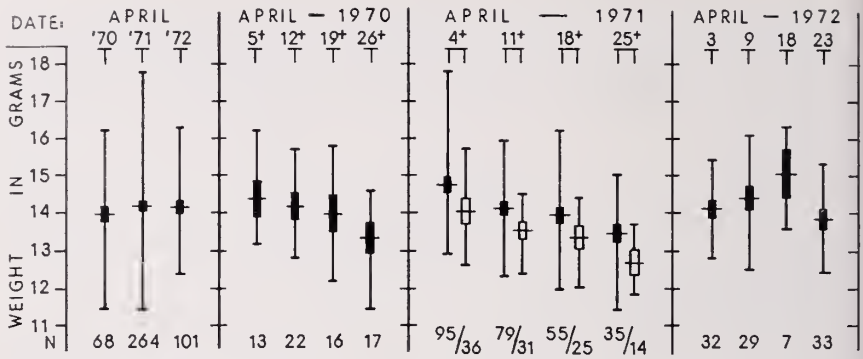

Fig. 7. Comparison of weights from each April of 3 years. Conventions as in Fig. 1. First panel presents total sample of males for each year. Remaining panels present samples by individual weekends, "+" following date indicates 2 days combined.

Variations between consecutive weekends.—With sizeable samples available, the male weights were studied in hourly periods on the first 3 weekends of April 1971 (Fig. 8). Within each weekend, the hourly changes were not significant, but each weekend showed a different pattern and significant changes in certain mean weights. On 4–5 April, the mean increased through the morning hours, typical of the changes seen thus far. On 11 April, mean weights started to rise, but then dropped, so that at 10:00 the mean was significantly lower than at the same hour on the prior weekend. On 18 April, the number of birds captured in the first 3 hours dropped drastically, but the mean weight of these few birds had not changed from the previous weekends. However, at both 10:00 and 11:00, the weights had decreased and both were significantly lower than they had been on 4–5 April. When considered collectively, these weekends indicate a general downward trend in April mean weights as had been noted in Fig. 7, but examined individually, they provide details on the gradual loss of weight.

Variations between successive days.—It is rare that birds are captured on 2 successive days in numbers large enough to permit analysis, but in 1971 I captured 55 males and 18 females on 4 April and 40 males and 18 females on 5 April (Fig. 9). By the test used, the mean weight of each sex did not increase significantly, although on the second day, the males had gained 2.7% and the females 3.6% which is counter to the downward trend noted in Fig. 7. When male weights were plotted by the hour for each day, the changes were not significant, but a comparison of the first and last mean indicated a gain of 5 to 6% occurred through each morning.

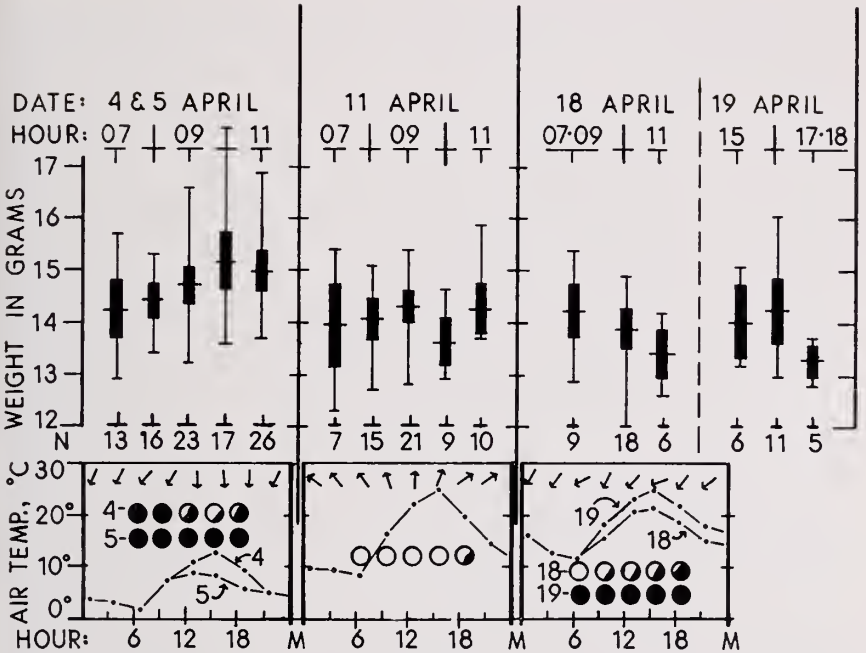

Fig. 8. Weights of males from first 3 weekends of April 1971 presented by hour of capture on specific date. Conventions as in Fig. 1. Lower panels summarize weather observations at three-hour intervals on date of capture. Arrows indicate wind direction on weekend, north at top of figure. Circles indicate sky conditions: filled circles = fully overcast skies; open circles = no clouds; partially filled circles = % of clouds to clear sky. Temperatures presented by connected dots. Number inside panel is date of weather if different patterns occurred.

which is equal to the gain in March (Fig. 5-B) when temperatures were much lower. Also, the mean weight for each hour was consistently higher on the second day. If all conditions were equal, the Laws of Chance (Moroney 1951) imply this could happen only once in 32 cases ($P = 0.04$). But, were all conditions equal? I suggest that weather had effected this result.

Effects of weather on mean weights.—It has been demonstrated that mean weights are inversely correlated with ambient temperatures on a long-range basis (see above). My findings suggest that birds are also sensitive to immediate changes in weather conditions, possibly to the availability of solar radiation and to wind velocity, and that they respond immediately with short-lived changes in mean weight.

With sex, age, and hour of capture described, I examined the weights

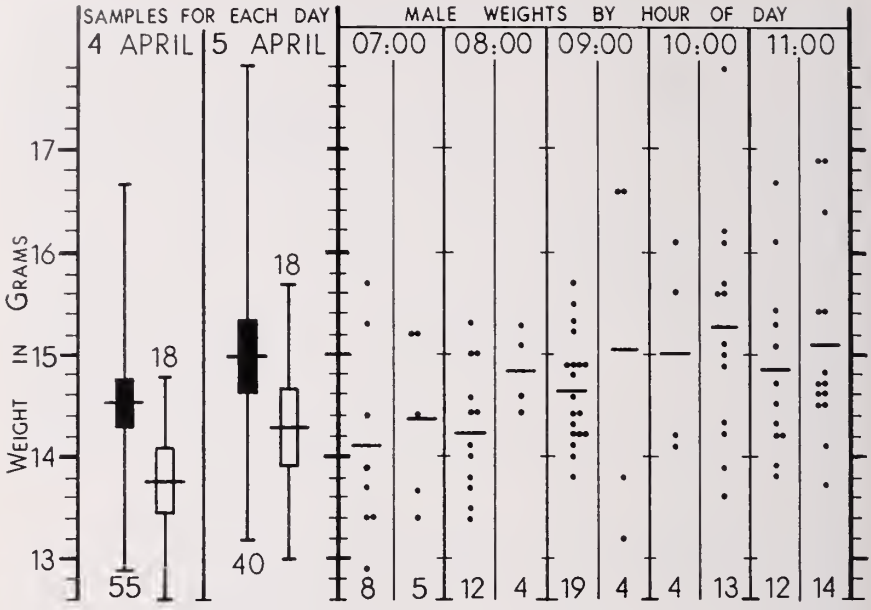

Fig. 9. Body weights from 4 and 5 April 1971. First panel compares sample of each sex from individual days. Final panel presents weights of individual males (dots) by hour of capture with simple mean (horizontal line) for each day, 4 April to left and 5 April to right. Numbers at bottom are sample sizes. Conventions as in Fig. 1.

of April 1971 for effects of changes in weather (summarized in Fig. 8). As mean temperatures for each weekend (7°, 14°, and 17°) were increasing, mean weights were decreasing (Fig. 7). However, slight variations in weight could not be related to temperature changes alone. On 4–5 April, barometric pressure and wind direction were unchanged as mean temperature dropped a mere 2° on 5 April. However, mean wind velocity increased from 15 km/hr on 4 April to 31 km/hr on 5 April and this, coupled with a lack of sunshine, may have effected at least part of the increased weights shown in Fig. 9.

On 11 April, with higher temperatures, less wind, and clear skies, the birds initially came in fair numbers, then feeding activities subsided (Fig. 8). With similar weather on the following day, the birds ignored the food in our traps. A week later, on 18 April, the birds came in small numbers as the temperatures were high and the skies mostly clear. But on 19 April, (we could not work the traps in the morning) the temperatures were even higher, yet the birds came in fair numbers in the late

hours, possibly ingesting more food as a reaction to stronger NNE winds and overcast skies.

Similar reactions to the lack of solar radiation were found in March 1970. The first 2 weekends (mean 8°C) were about 5°C above normal. On 1 March, with no sunshine available, the weights were high (Fig. 5); whereas they were significantly lower on 8 March with 90% available sunshine. On the next 2 weekends, we had fog and overcast skies each day. On 15–16 March, mean temperatures dropped to –4°C and –6°C with winds NNW at 15 to 25 km/hr and light snow, so all species were actively feeding and goldfinch weights were again high. On 22–23 March, however, mean temperature (4°C) was higher, winds were slower at 10 to 15 km/hr, but weights were still high. It is impossible to say that sky conditions were responsible for all of the increase, but higher temperatures did not produce a drop in weight that would be expected.

Feeding activities at this station have been noted, when temperatures remain unchanged at lower levels, to be inversely proportional to the availability of sunshine (solar radiation). Apparently, small birds are sensitive to solar radiation and wind velocity and direction, and these effect minor, short-term fluctuations in weights.

Relation of wing chord to weight variations.—Most authors (Connell et al. 1960, Mascher 1966, Rogers and Odum 1964) have used the wing chord or flattened wing measurement as an indicator of size of the bird's framework and some have found no differences in the fat-free weight due to sex or age if the wing measurements were the same. However, Nolan and Mumford (1965), working with migrating warblers of TV tower kills, stated, "... coefficients of correlation of wing length and total weight emphasize the lack of constancy in the relation when weight includes fat," and added, "Significant differences existed in average measurements and weights; in some instances the differences were related to both age and sex, in some to only one of these variables."

With this in mind, I separated the goldfinches by sex, age, and wing length and determined the mean body weight of these at various time periods, some of which are presented in Fig. 10. In the top panel, September data are presented first. With fresh plumage the HY males were rather evenly distributed through the range of wing sizes, and the mean weights increased in correlated, orderly steps. All samples tended to show this, but few samples showed a relationship as well coordinated as this. In October, the individual weights of HY birds varied considerably, some young were self-dependent and late hatched parent-dependent young were also present, and the wing/weight relation was obscured. A few adult males, now molting, were about 2 g heavier than adult females, not yet

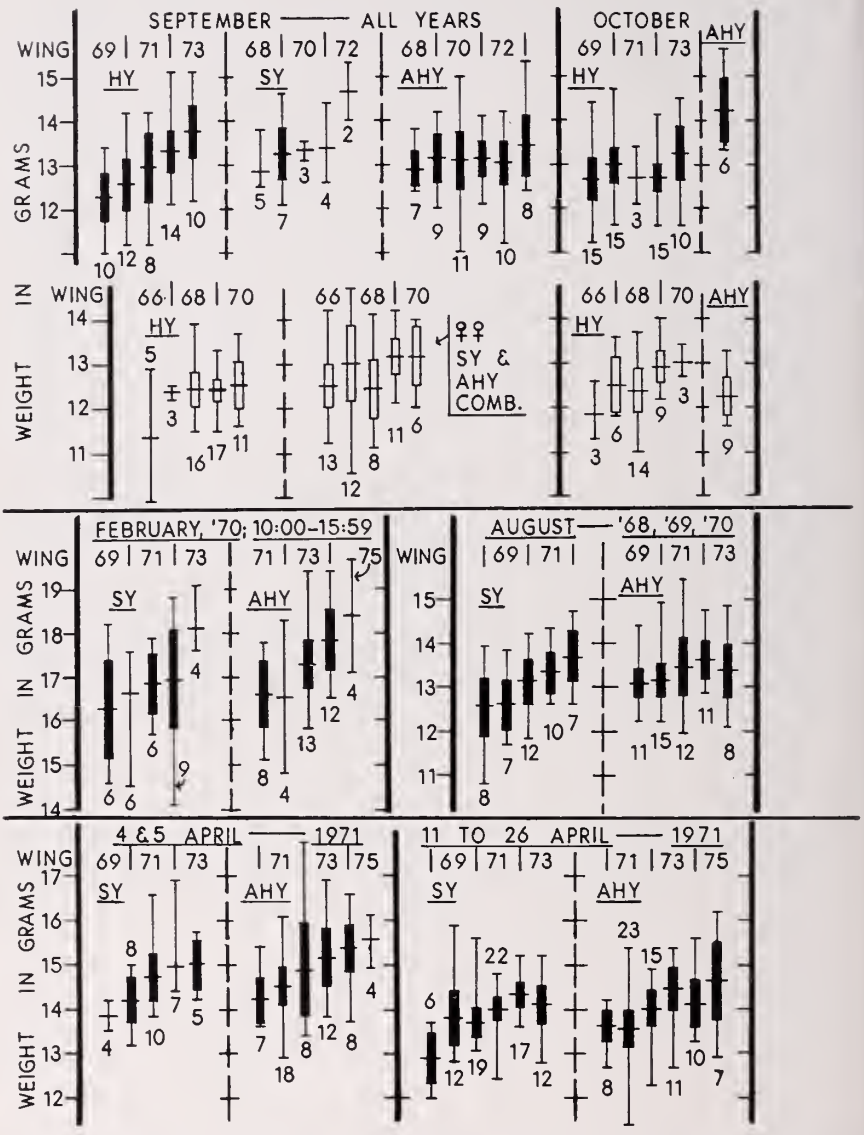

FIG. 10. Selected examples of wing chord/weight relations. Samples from various dates or time periods were divided by wing chord lengths, then weights were calculated for each sample. Conventions as in Fig. 1.

molting, while HY males were only about 0.5 g heavier than HY females. While females tended to follow the correlated pattern, because of smaller samples, disproportionate importance was given to the individual bird, breeding condition, molt, and/or feather wear.

When the February SY males were compared to the September HY males, each group by wing size was noted to have added essentially the same amount of weight (about 4 g). By August, the SY males were about the same weight as they had been the prior September; however, the wing measurements had been reduced about 1.5 mm. (In Fig. 4, by comparing HY and SY birds in September, the loss was determined as 1.7 mm for the year.) In comparing age groups, the February males showed a noticeable difference. Although the weights were fairly evenly matched, the AHY birds had measurements about 2 mm longer than those of the SY birds (note the scales on wings are not identical). By April, the difference had narrowed to about 1.4 mm. In Fig. 4, September wing chords were only about 1 mm longer on the AHY birds. Apparently, the factors of feather wear relative to age, sex, nesting, and molt may have some slight influence on the wing/weight relationship, and the rate of wear may not be constant throughout the year in the various groups.

In the lower panels of Fig. 10, males from 4–5 April 1971 produced similar patterns in both age groups, but birds taken from the following 3 weekends of April 1971 failed to show this relationship. It seems temporal consolidation of the samples is important to this study. Also, hour of capture can play upon the results. Note that the February 1970 samples were restricted to the hours after 10:00; when I included weights from earlier hours, the relationship was obscured.

SUMMARY

During a general banding program conducted on weekends for 5 years at the Cincinnati Nature Center, weights and wing chord measurements of American Goldfinches were recorded. From this, 1448 weights of 978 males and 756 weights of 538 females were obtained, treated as separate populations, and divided into age-related samples representing various time and biological periods. The means ± 2 S.E. were used to make simple comparisons between seasons, weekends, days, and hourly periods.

A comparison of weights by months showed weights were inversely related to temperature. Evidence of an increase in weight during molt was noted. During the summer, the lowest (basic) mean weights were attained (12.5 g for males and 12.4 g for females), and both sexes gained about 4% during the day. During the breeding season the females gained 7.3% and males gained 4.9% above the basic mean weight. In February, the male mean weight was 35.6% and the female mean was 34.4% above the basic mean weight. At this time males gained 19% during the day, but in March they gained only 5.5% in a day. Fat classes (deposits) were shown to change paralleling the hourly changes in mean weight.

The date of capture and mean weights were not correlated. The hour of capture produced significantly lower mean weights in the earlier hours of the colder months, but not in the warmer months. The handling of birds appeared to reduce the gain in diurnal weight during February and March. Variations in mean weights between various years in selected months were found to be related to hour of capture or weather in some cases.

The effects of weather were demonstrated. Changes in solar radiation, wind direction and velocity, and immediate changes in temperature seemed to affect weight and feeding activities in hourly and daily periods.

The ratio of total weight to wing chord was shown to vary with season, sex, and age. In both sexes, the newly fledged young had significantly longer wing chords than most adults of their sex.

ACKNOWLEDGMENTS

I am especially indebted to B. Franklin McCamey who introduced me to the principles of banding and inspired a serious approach to the project, then assisted and advised with many technical problems. Through the years, Richard Durrell and the Trustees of the Cincinnati Nature Center encouraged this research and made it possible by providing working space and special privileges in the use of the Nature Center land areas, for which I am grateful. The friendly cooperation of the staff and members of the Nature Center for their many favors and courtesies is gratefully acknowledged, especially their attentiveness to providing feed for our traps throughout the project.

Mary H. Clench contributed unlimited and extremely valuable assistance which made this paper possible, and I am indebted to her. DeVere E. Burt and Chandler S. Robbins provided suggestions on the figures. Jack L. Gottschang and the staff of the University of Cincinnati provided access to the University's computer and advised in this work. My wife, Virginia K. Wiseman, provided cooperation and support at every step in many ways to make this paper possible. Jay M. Sheppard introduced me to computer manipulation of the data. Jean K. Cassell provided much needed typing assistance. Funds received in 1974 through the Margaret Morse Nice Award from the Wilson Society provided partial assistance.

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cincinnati museum of natural history, 1720 gilbert avenue, cincinnati, oh 45202. accepted 26 dec. 1974.

GENERAL NOTES

Nine new specimen records for Guatemala.—During the course of field work on the ecology of arthropod-borne viruses in Guatemala, particularly in the environs of La Avellana on the Pacific lowlands, Department of Santa Rosa, I collected 9 species of birds not previously taken in Guatemala.

La Avellana is on the inland edge of a marsh that extends approximately 100 km along the Pacific coast. At La Avellana the marsh is about 2 km wide and is bordered on the seaward side by a barrier beach, on which is located the village of Monterrico. The marsh is composed of extensive areas of cattail, shallow (seasonally dry) lagoons, with mangroves along the major tidal channels. The marsh is more saline during the dry months December to May. A narrow, interrupted band of swamp forest borders the inner edge of the marsh and extends in a narrow riparian band as a gallery-type forest along streams draining into the marsh. Inland from La Avellana and extending parallel to the coast southeast into El Salvador and northwest towards San Jose is a belt (at La Avellana 3–5 km wide) of dry tropical scrub forest. This narrow belt was not plotted on the map of the Holdridge Life Zones of Guatemala (Land, Birds of Guatemala, Livingston Publ. Co., Wynnewood, Pa., 1972:7, map II) but is evident on distributional maps of moist forest inhabiting species such as the Longtailed Manakin (*Chiroxiphia linearis*) (p. 202) or the Rufous-browed Peppershrike (*Cyclarhis gujanensis*) (p. 270). Farther inland more mesic tropical dry forest grades into the tropical moist forest of the foothills. On map IV (Land, op. cit.:21) localities 44 and 45, representing La Avellana and Papaturro are reversed; 44 should be La Avellana.

I worked at La Avellana during February and August 1968, July and August 1970–1972 and in April and early May 1973 and 1974, and collected less extensively elsewhere in Guatemala within these time periods. C. Donald Powers participated in the field work in 1971 and 1972, John O. Biderman in 1973, and Ronald C. Franck in 1974.

Specimens are deposited at the American Museum of Natural History or at Cornell University, Ithaca, New York.

Puffinus griseus. Sooty Shearwater. A male found dying on the beach at Monterrico, 8 May 1974 and obtained from a native is the first specimen for the family Procellariidae from Guatemala. In mid-April 1973 Jehl saw an (?) individual about 40 km off the Pacific coast of northwestern Guatemala (Auk 91:681–699, 1974).

Cathartes burrovianus. Yellow-headed Vulture. An adult male with testes slightly enlarged was collected ca. 7 km W of La Avellana, 25 November 1969. On that date at least 4, possibly 6 were seen. One or 2 were observed over the open marsh near La Avellana 19 July 1970 and occasionally on trips to this habitat during April and May 1973 and 1974.

Porzana flaviventer. Yellow-breasted Crake. This species was added by Eugene Eisenmann to Land's manuscript of "Birds of Guatemala." This was based on information from Miguel Alvarez del Toro (*pers. comm.*) regarding specimens I collected at the Laguna Lagartos on the Guatemala-Mexican border 22 January 1966. However, those specimens were taken on the Chiapas side of the marsh (see Dickerman, Wilson Bull. 83:53, 1971) and by Land's criteria the species probably should have been considered hypothetical for Guatemala at that time. Definite Guatemala records are now available. I saw 2 in the marsh near La Avellana and collected an

adult female 29 April 1974. Its ovary was granular although only slightly enlarged. The bird weighed 20.2 g.

Charadrius alexandrinus. Snowy Plover. I saw 2 birds and collected one at the mouth of the Rio Los Esclavos, Department of Santa Rosa, 28 April 1973. The specimen was an excessively fat female that weighed 50.4 g.

Limosa haemastica. Hudsonian Godwit. Two birds were collected from a flock of 14 that I flushed from mud flats in the shallow lagoons lying between Avellana and Monterrico on 26 April; 1 to 8 birds were observed 27–29 April 1973. A group of 3 collected 24 April 1974 were the only ones seen that spring. The 2 females collected in 1973 were fat and weighed 252 and 220 g; those taken in 1974, 2 females and a male, all were moderately fat to fat and in heavy molt; they weighed 192.6, 204 and 188 g respectively.

Hydroprogne caspia. Caspian Tern. This species was included by Land based on a Pacific coast sight record made 15 February 1967. Additional records are 2 seen near La Avellana 25 November 1969, 20–50 seen nearly daily 10 April to 6 May 1973, and 1–30 seen nearly daily 6–29 April 1974. One was collected 12 April, thus removing the species from the hypothetical list.

Philomachus pugnax. Ruff. A Reeve was collected on the mud flats in the marsh between La Avellana and Monterrico 16 April 1974. She was in heavy molt about the head, and was without fat (weight 68 g). The ovary was not enlarged but ovules were distinct. The meat was dark and flavorsome, comparable to that of *Limnodromus* and *Numenius.* This is apparently the southernmost verified record of the species in Central America.

Otus cooperi. Pacific Screech-owl. Land (op. cit.) mentioned that this screech-owl was to be expected in Guatemala. A female was collected from a pair by Sergio Romero Ibarra 2 km NE of Papaturro, (*ca.* 5½ km E of La Avellana) 2 May 1974. She weighed 181 g.

Cassiculus melanicterus. Yellow-winged Cacique. This species, formerly considered restricted to Mexico, is common in the riparian zones transecting the arid tropical scrub inland from La Avellana. I saw groups of 30 or more birds feeding in fruiting trees. Nest building was under way in late April 1974. Specimens were collected 6 August 1971, 14 and 29 August 1972 and 11 April 1973.—Robert W. Dickerman, *Dept. of Microbiology, Cornell Univ. Medical College, 1300 York Ave., New York, NY 10021.* *Accepted 26 Nov. 1974.*

A new species of *Spizaetus* from the Pliocene of Nebraska.—The late Pliocene (Kimballian) of Nebraska is producing a rich avifauna which has so far included a small turkey, *Proagriocharis kimballensis* (Martin and Tate, Wilson Bull. 82:214–218, 1970), a goose-like swan, *Paracygnus plattensis* (Short, Am. Mus. Novitates 2369:1–7, 1969), and a giant anhinga, *Anhinga grandis* (Martin and Mengel, Auk 92:137–140, 1975). I will here describe a new species of long-shanked eagle, represented by a tarsometatarsus. The fauna of the Kimballian in Nebraska and a brief history of the "*Amebelodon fricki* Quarry" (Univ. of Nebraska State Museum UNSM collecting locality Ft-40) where this specimen was found, is summarized in Schultz et al. (Bull. Univ. Nebraska State Mus. 9:1–31, 1970).

Comparisons were made with tarsometatarsi of *Geranoaetus melanoleucus* (2 specimens), *Buteo harlani* (5), *B. swainsoni* (5), *B. regalis* (50), *B. jamaicensis* (50), *B. buteo* (2), *B. lineatus* (3), *B. platypterus* (3), *B. nitidus* (5), *B. magnirostris* (10), *B.*

lagopus (20), *Buteogallus anthracinus* (5), *Parabuteo unicinctus* (4), *Leucopternis albicollis* (1), *Hypomorphnus urubitinga* (1), *Haliaeetus leucocephalus* (1), *Aquila chrysaetos* (1), *Spizaetus ornatus* (1), *S. cirrhatus* (1), *S. tyrannus* (1), *S. tanneri* (holotype), *S. grinnelli* (4), and *Morphnus woodwardi* (3).

The fossil tarsometatarsus is larger than in any living species of North American *Buteo*. It is elongate as in *Parabuteo* or *Geranoaetus*, but not as elongate as in *Hypomorphnus*. It resembles *Spizaetus* rather than *Buteo*, *Parabuteo* or *Geranoaetus* in the following: (1) the inner proximal foramen lies along the medial side of the inner calcaneal ridge (this character is variable, but held in 145 of the 151 tarsometatarsi of *Buteo* examined); (2) the sides of the tarsometatarsus slope inward gradually; (3) the position of the tubercle for tibialis anticus is more distal; (4) the antero-proximal face of the shaft is flattened on the internal margin for a greater distance distally; (5) the external and internal calcaneal ridges extend farther distally; (6) the external border of the shaft curves posteriorly; and (7) the shaft is less constricted distally.

Leucopternis differs from the fossil in having a more slender shaft. In most respects the new fossil closely resembles *Spizaetus grinnelli* and may be best placed in the genus *Spizaetus*.

Spizaetus schultzi, sp. nov.

(Fig. 1)

Holotype.—Right tarsometatarsus, lacking only part of the inner calcaneal ridge UNSM 20041, from Coll. Loc. Ft-40, E ½ SW ¼ Sec 15, T5N, R26W, 9.6 km N and 10.2 km W of Cambridge, Frontier Co., Nebraska, from the Sidney Gravel Member of the Kimball formation, Ogallala Group, Pliocene.

Diagnosis.—The tarsometatarsus of *Spizaetus schultzi* is near the minimal size given for the tarsometatarsus of *S. grinnelli* by Howard (Carnegie Inst. Washington Publ. 429: 1–89, 1932). It differs from that species in having: (1) proximal end more compressed antero-posteriorly; (2) external calcaneal ridge diverging laterally in proximal view and extending distally as a thin ridge; (3) distal end with middle trochlea narrower and extending farther proximally and anteriorly; (4) trochleae slightly more arched. *S. schultzi* is larger than *S. tyrannus*, *S. ornatus*, and *S. nipalensis*, but it is smaller and less massive than the fossil species *S. willetti* and *S. tanneri*. Measurements of the type specimen (a phalanx) of *S. pliogryps* given by Howard (Carnegie Inst. Washington Publ. 551:141–149, 1946) indicate that it too, was a much larger bird than *S. schultzi*.

Description.—A long-shanked eagle about the size of a male *Geranoaetus melanoleucus*; proximal end of tarsometatarsus broad with shallow cotylae; internal cotyla nearly circular; external cotyla oval and extending anteriorly past intercondylar tubercle; intercondylar tubercle broad and low; inner calcaneal ridge of hypotarsus short, thick, and extending further distally than in *Geranoaetus*; small inner proximal foramen medial to distal end of inner calcaneal ridge; inner proximal foramen small; proximal foramina set anteriorly in a deep depression which undercuts the articular surface as in *Aquila*; medial side of proximal end of bone excavated about as in *Aquila chrysaetos*; tubercle for tibialis anticus proximally located as in *Spizaetus*; extensor groove leading into distal foramen deep and well defined as in *Spizaetus*; facet for metatarsal I slightly larger than in *Geranoaetus melanoleucus*, and trochleae more arched; medial face of trochlea fairly short and stout; middle trochlea narrower and extending further proximally than in *Geranoaetus* and with base more constricted when viewed posteriorly; lateral ridge of external trochlea rounded. The following measurements are (in mm) from the holotype:

FIG. 1. *Spizaetus schultzi*, holotype, right tarsometatarsus, UNSM 20041. From left to right: anterior, distal, proximal, and posterior views, ×1.

total length 103, distance from distal end of middle trochlea to center of the tubercle for tibialis anticus 80.5, width of proximal end 17.6, depth of proximal end excluding calcaneal ridges 8.1, width of distal end 18.8, depth of middle trochlea 8.2.

Etymology.—Named for C. B. Schultz in recognition of his contributions to our knowledge of the North American Pliocene.

Discussion.—A few other fossil eagles warrant comparison with *Spizaetus schultzi*. The late Pleistocene *Morphnus woodwardi* (Howard 1932) has a much larger, more massive tarsometatarsus with a wider shaft than in *S. schultzi*. It has the tubercle for tibialis anticus more proximally placed and the facet for metatarsal I larger, forming a distinct notch on the medial side of the shaft. It also has the trochleae less arched with the internal trochlea strongly directed medially. *Buteo contortus* from the late Miocene of Nebraska resembles *Morphnus woodwardi* and differs from *Spizaetus schultzi* in these respects. *Buteo contortus* also differs from most other buteos in having the inner proximal foramen medial to the inner calcaneal ridge (Wetmore, Bull. Amer. Mus. Nat. Hist. 48: 483–507, 1923).

Buteo conterminus from the early Pliocene of Nebraska is larger than *Spizaetus schultzi*, has the facet for metatarsal I more proximally situated, the outer ridge of the external trochlea less extended posteriorly, and the trochleae less arched (Wetmore 1923).

Buteo typhoius from the Upper Miocene of Nebraska (Wetmore 1923) has a more distinct anterior groove on the face of the shaft, the shaft thicker antero-posteriorly, and the external trochlea larger and more blunted posteriorly than in *Spizaetus schultzi*.

Buteo fluviaticus (Miller and Sibley, Condor 44:39–40, 1942) from the Oligocene of Colorado has the shaft of the tarsometatarsus wider above the trochleae, the middle trochlea larger, and the trochleae less strongly arched than in *S. schultzi*.

Buteo antecursor (Wetmore, Bull. Mus. Comp. Zool. 75:297–311, 1933) from the Upper Oligocene of Wyoming has a less elongate tarsometatarsus than *Spizaetus schultzi*, and *B. ales* (Wetmore, Ann. Carnegie Mus. 16:403–408, 1926) from the lower Miocene of Nebraska is smaller and has the trochleae less arched.

This is the second record of *Spizaetus* from the Central Great Plains and the oldest reported occurrence of the genus. The other record from this region and the next oldest occurrence is *S. tanneri* from the Blancan of Nebraska (Martin, Condor 73:248–250, 1971). North American fossil species of *Spizaetus* fall into 2 groups: large massive forms which seem similar to *Aquila* (*S. tanneri*, *S. willetti*, and *S. pliogryps*), and smaller more lightly built forms (*S. schultzi* and *S. grinnelli*).

I am indebted to C. B. Schultz for the privilege of studying the fossil birds in the collections of the University of Nebraska State Museum, to R. M. Mengel and M. A. Jenkinson for critically reading the manuscript, and to D. K. Bennett for the illustrations.
—Larry D. Martin, *Museum of Natural History and Dept. of Systematics and Ecology, Univ. of Kansas, Lawrence 66045.* *Accepted 19 Nov. 1974.*

The bony stapes in the Upupidae and Phoeniculidae: evidence for common ancestry.—Krause (Die Columella der Vögel, Berlin, R. Friedländer and Sohn, 1901) examined the form of the avian bony stapes in a number of groups, but no comprehensive study has yet been achieved. As I reported earlier (Feduccia, Auk 91:427–429, 1974), most of the nonpasserine orders, and the entire "oscine" passerine assemblage of birds possess a bony stapes resembling the primitive reptilian condition, with a flat footplate, and a straight bony shaft. This type of stapes (Fig. 1) no doubt represents the retention of the primitive condition. Both the New and Old World suboscines possess a characteristic derived morphology of the bony stapes, and this I interpreted (op. cit.) as evidence for common ancestry of the Old and New World groups. In the examination of the coraciiform families (to be presented in detail later) I discovered that the Hoopoe (Upupidae: *Upupa epops*) and the wood-hoopoes (Phoeniculidae: *Phoeniculus purpureus* and *Rhinopomastos cyanomelas*) also possess a common derived morphology of the bony stapes which is found in no other of the more than 1000 species I have examined. This type of stapes (Fig. 1) is characterized by a flat bony footplate, but with a short but wide shaft that bifurcates into 2 processes. There is a long, laterally directed thin process, and a shorter, broad process, both of which connect to the tympanic membrane via extracolumellar ligaments, and no doubt function in a complex lever system.

The possession of this bizarre type of stapes in both the Upupidae and Phoeniculidae I interpret as a strong indication of monophyly of the 2 groups that points *a fortiori* to

FIG. 1. Alizarin-stained stapes of A, *Upupa epops* (Upupidae); B, *Phoeniculus purpureus* (Phoeniculidae); C, *Leptosomus discolor* (Leptosomatidae); D, *Coracias noevia* (Coraciidae); and E, *Berenicornis albocristatus* (Bucerotidae). The stapes of *Phoeniculus* is slightly damaged. C, D, and E represent the primitive condition for birds; *Colius* has a similar stapes. All approximately × 10–30.

their uniqueness. Because of this very unusual common character, and because there are few "good" characters to ally them with the other members of the Coraciiformes, I suggest that they are best treated as 2 families within an order Upupiformes, as Stresemann (Aves. *In* Handbuch du Zoologie, vol. 7, No. 2, W. deGruyter, Berlin, 1927–34) suggested, but that the hornbills (Bucerotidae) not be included within the order until evidence for evolutionary affinity can be aptly demonstrated. Whether or not the woodhoopoes and Hoopoe are considered as separate families or subfamilies of a Upupidae is a matter of arbitrary decision.

This research was supported by a grant from the University of North Carolina Research Council. R. W. Storer (Univ. of Michigan), and R. L. Zusi (National Museum of Natural History) kindly permitted me to use collections under their care.—ALAN FEDUCCIA, *Dept. of Zoology, Univ. of North Carolina, Chapel Hill 27514.* *Accepted 19 Dec. 1974.*

Morphology of the bony stapes in the Menuridae and Acanthisittidae: evidence for oscine affinities.—The Menurae comprise one of the 4 suborders of passerine birds. For the past century it has contained 2 species of lyrebirds in a family Menuridae, and 2 species of scrub-birds in a family Atrichornithidae; both families have been considered "suboscine" on the basis of syringeal anatomy (Ames, Peabody Mus. Nat. Hist. Bull. 37, 1971). The Menurae have been placed taxonomically usually next to, but at the end of the list of the suboscine assemblage. The New Zealand wrens (Acanthisittidae, 3 living species) have also been placed with the suboscines on the basis of syringeal anatomy, but within the suborder Tyranni. Sibley (Emu 74:65–84, 1974) has concluded on the basis of both anatomical and egg white protein evidence (IFAG patterns) that the lyrebird is not suboscine, but is allied with the bowerbird-bird-of-paradise assemblage. Sibley had not examined the egg white proteins of *Atrichornis*, but because of its anatomical similarity to *Menura* he suggested that it be tentatively retained in a family next to the Menuridae. His major taxonomic conclusion was that the suborder Menurae be dropped, and the Menuridae and Atrichornithidae be placed next to the Ptilonorhynchidae in the suborder Passeres.

The vast majority of birds (most of the nonpasserine orders, and the entire "oscine" assemblage) possess the primitive condition for the avian stapes, with a flat footplate, and a straight bony shaft; this type of stapes does not differ significantly from the same bone in reptiles. On the other hand, the "suboscines" (Furnariidae, including the woodhewers, Formicariidae, Conopophagidae, Rhinocryptidae, Cotingidae, Pipridae, Tyrannidae, Phytotomidae, Eurylaimidae, Pittidae, and Philepittidae) all possess a derived mor-

FIG. 1. Alizarin-stained stapes of A, *Smithornis capensis* (Eurylaimidae); and B, *Pitta reichenowi* (Pittidae). Approximately × 30.

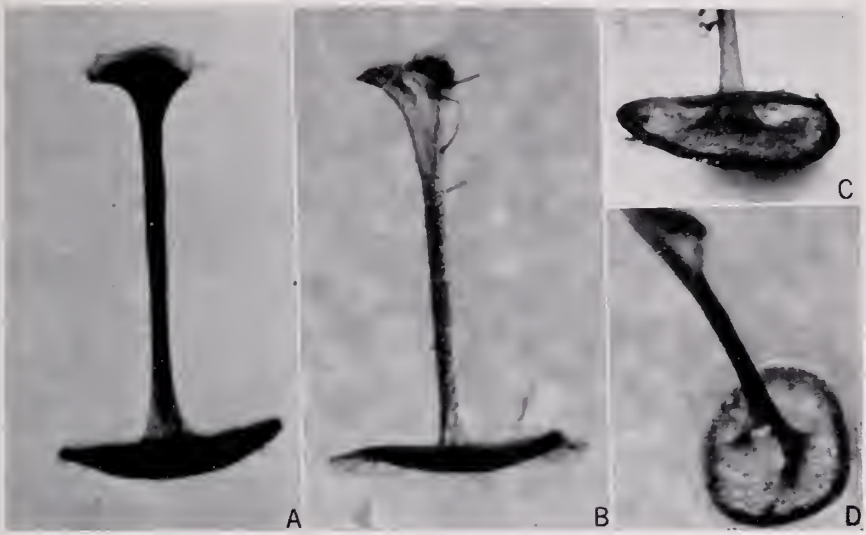

FIG. 2. Alizarin-stained stapes of A. *Menura superba*; B. *Irena puella* (Irenidae); C, footplate of *Menura* stapes; D. footplate of *Irena* stapes. Approximately × 20.

FIG. 3. Stapes of *Acanthisitta chloris* (Acanthisittidae). The footplate of the stapes was half out of the oval window, but still clinging by dried connective tissue. Photo from an unnumbered skull from the British Museum of Natural History. × 20.

phology of the stapes (Fig. 1) with an expanded bulbous footplate area perforated usually by one (often 1 large and 1 small) fenestra (Feduccia, Auk 91:427–429, 1974). I have recently had the opportunity to examine the stapes in the lyrebird (*Menura superba*) and the New Zealand wren, the Rifleman (*Acanthisitta chloris*); both possess the primitive condition for the element. The stapes of *Menura* (Fig. 2) is illustrated next to that of the leafbird, *Irena*, a typical oscine. The stapes of *Acanthisitta* (Fig. 3) is also typically oscine, but with a shaft relatively more robust than those shown in Fig. 1.

Sibley's (1974 op. cit.) biochemical data, along with the evidence from the stapes compel me to conclude that lyrebirds are oscine, and are likely close to the bowerbird-bird-of-paradise assemblage. Additional *new* evidence will be needed to draw conclusions of the relationships of the New Zealand wrens, but at present I suggest that their closest living relatives are to be found among the oscines.

I wish to thank Dr. Charles G. Sibley for providing me with a specimen of *Menura* and encouraging this study. Dr. R. L. Zusi kindly permitted me to examine a specimen of *Acanthisitta* on loan to him from the British Museum (Natural History), and arranged for the photography of the specimen (Fig. 3). I continue to be indebted to Dr. R. W. Storer (Univ. of Michigan) and Dr. R. L. Zusi (National Museum of Natural History) for permitting me to examine specimens under their care. This study was supported by a grant from the University of North Carolina Research Council.—Alan Feduccia, *Dept. of Zoology, Univ. of North Carolina, Chapel Hill 27514.* *Accepted 19 Dec. 1974.*

Additional observations on hover-feeding by North American ardeids.—In a previous note (Rodgers, Wilson Bull. 86:70–71, 1974), I reported observing Snowy Egrets (*Egretta thula*) and Great Egrets (*Casmerodius albus*) hover-feeding in Barataria Bay, Louisiana. Since that time, I have observed Louisiana Herons (*Hydranassa tricolor*), Little Blue Herons (*Florida caerulea*), and a Black-crowned Night Heron (*Nycticorax nycticorax*) hover-feeding in Barataria Bay with Snowy and Great Egrets, Ring-billed Gulls (*Larus delawarensis*), Laughing Gulls (*Larus atricilla*), Forster's Terns (*Sterna forsteri*), Royal Terns (*Thalasseus maximus*), and Sandwich Terns (*Thalasseus sandvicensis*). These birds were feeding on dead or dying fish on or near the surface of the water. The fish were discarded from boats trawling in the bay. Kushlan (Wilson Bull. 84:199–200, 1972) previously reported observing Louisiana Herons aerial feeding with Snowy Egrets at a fresh-water pond, and Reese (Condor 75:352, 1973) reported Great Blue Herons (*Ardea herodias*) and Great Egrets feeding together on dead fish from the surface of Chesapeake Bay.

The behavior of all 5 species of ardeids hover-feeding on Barataria Bay was identical. On approaching the fish, the heron would hover, extend its head downward, and pick up the fish with its mandibles. At this time the legs of the heron usually dangled below its body with the feet often completely submerged.

One to 5 Louisiana and Little Blue herons were observed hover-feeding on 7 and 3 occasions respectively. Hover-feeding by the Black-crowned Night Heron was observed only once about one hour before sunset. The Louisiana Herons, Little Blue Herons, and the Black-crowned Night Heron were observed hover-feeding along with as many as 70 Snowy Egrets and 15 Great Egrets.—James A. Rodgers, Jr., *Museum of Zoology, Louisiana State Univ., Baton Rouge 70803. Present address: Dept. of Biology, Univ. of South Florida, Tampa 33620.* *Accepted 17 Jan. 1975.*

Additional records of unusual nectar feeding.—Recent notes (Fisk, Auk 90:208–209, 1973; Leck, Auk 91:162–163, 1974) on nectar feeding by orioles have prompted me to record observations on such feeding by orioles and 8 other species of birds.

At a hummingbird feeder filled with red-colored sugar water and maintained near Joshua Tree, San Bernardino Co., California, Scott's Orioles (*Icterus parisorum*), both adults and immatures, have fed regularly. Also, I have seen House Finches (*Carpodacus mexicanus*) feeding, but the size of the exit hole for the liquid precludes regular feeding by this species. Cactus Wrens (*Campylorhynchus brunneicapillus*) also have been observed feeding from this feeder. On occasion Scrub Jays (*Aphelocoma coerulescens*) have tried to feed, but since they cannot insert their bills, they can feed only when some of the liquid is spilled.

At Santa Monica, Los Angeles Co., California, I have occasionally seen the Plain Titmouse (*Parus inornatus*) drinking the red-colored sugar water from my aviary feeder. Hooded Orioles (*Icterus cucullatus*) and Northern (= "Bullock's") Orioles (*Icterus galbula*) are summer residents in the area but neither species has been seen using the feeder. Commercially designed and manufactured for orioles (much enlarged fluid exit holes), this feeder is so arranged that perches and exit holes are available to both wild and caged birds. Zebra Finches (*Poephila castanotis*) and Cutthroat Finches (*Amadina fasciata*) have fed on the sugar water whereas Orange-cheeked Waxbills (*Estrilda melpoda*) and a Pintailed Whydah (*Vidua macroura*) have not been seen to feed.

Both Fisk (op. cit.) and Leck (op. cit.) have emphasized that nectar feeding is a regular behavior for many orioles. Indeed, this is recognized by the fact that one can purchase commercially manufactured "oriole feeders." Also, Wible (Auk 91:418–419, 1974) has recently reported apparent feeding on possibly nectar-filled calyx capsules by a pair of Cardinals (*Cardinalis cardinalis*). An earlier note (Gullion, Auk 67:398–399, 1950) recorded probable nectar feeding by several *Carpodacus* finches. James D. Rising (pers. comm.) has observed Acorn Woodpeckers (*Melanerpes formicivorus*) and Mexican Jays (*Aphelocoma ultramarina*) feeding from an artificial source in Arizona. From these observations, it seems clear that many species of birds, even those which are primarily granivorous and which are not usually considered to be nectarivorous, may exploit such resources when convenient and recognizable.—George F. Fisler, *Dept. of Biology, California State Univ., Northridge 91324.* *Accepted 10 Dec. 1974.*

Nesting Indigo Buntings displaced by *Peromyscus*.— On 19 and 20 July 1974 we observed a female Indigo Bunting (*Passerina cyanea*) building a nest in a clump of evening primrose (*Oenothera biennis*) at the Rose Lake Wildlife Research Area in Clinton Co., Michigan. The nest was 65 cm above ground and located in a 2-year-old abandoned field dominated by perennial grasses. About 5 m east of the site was a 1-year-old abandoned field which still had much bare ground. The nest, located almost 100 m from the nearest woody vegetation, was considered atypical, since we found Indigo Bunting nests primarily in the wooded edges surrounding the field. We saw a male Indigo Bunting near the nest site, but it was not involved in nest construction.

The nest was briefly examined at 16:00 on 21 July when the Indigo Buntings were absent. It appeared to be almost completed. No eggs were present.

On 22 July at 11:30 we discovered that the opening of the nest had been roofed

over with grass stems and other herbaceous material. The cause of this modification was not determined until 11:15 on 23 July, when, while probing the nest with a pencil, a mouse (*Peromyscus* sp.) scurried out. On 24 July a mouse was again observed in the nest but escaped capture.

Most likely the nocturnal *Peromyscus* had occupied the nest on the night of 21 July causing the Indigo Buntings to abandon the nest before egg laying began. The displaced Indigo Buntings then apparently relocated at a new nest site, because shortly afterwards we noticed a female Indigo Bunting building a nest within the territory of the male less than 50 m from the old site.

This observation may be the first recorded instance of the nesting behavior of *Peromyscus* being a factor which could cause Indigo Buntings to abandon a nesting attempt. The mouse could have been either the prairie deer mouse (*P. maniculatus bairdii*) or the woodland-inhabiting white-footed mouse (*P. leucopus*). We found no published evidence of *P. m. bairdii* using bird nests for its own nest, but this subspecies is a capable climber under both field (Blair, Am. Midl. Nat. 24:289, 1940) and laboratory (Foster, J. Mammal. 40:496–513, 1959) conditions and could conceivably use such nests. On the other hand, nests of *P. leucopus* previously have been reported in deserted, open nests of the Gray Catbird (*Dumetella carolinensis*), Red-winged Blackbird (*Agelaius phoeniceus*), Wood Thrush (*Hylocichla mustelina*), and Red-eyed Vireo (*Vireo olivaceous*) (Audubon and Bachman, The quadrupeds of North America, Vol. 1. V. G. Audubon, New York, p. 302. 1849) and in cavity nests of chickadees (*Parus* sp.) (Edwards and Pitts, J. Mammal. 33:244, 1952) and woodpeckers (Picidae) (Metzger, J. Mammal. 36:104. 1955) during winter. Kendeigh (J. Wildl. Manage. 6:22, 1942) mentioned an open nest (species unidentified) destroyed by *P. leucopus* during the breeding season, and Stokes (Wilson Bull. 62:125, 1950) noted that 3 or 4 deserted nests of the American Goldfinch (*Spinus tristis*) were soon covered over and inhabited by *P. leucopus*. Stokes suspected that mice may eat eggs not being incubated. In no instance was there any mention that *P. leucopus* may actually occupy an active nest.

We thank R. H. Baker, B. D. J. Batt, D. L. Beaver, and L. W. Gysel for their comments. These observations were made while JEG was involved in a McIntire-Stennis project.—J. Edward Gates and Donna M. Gates, *Dept. of Fisheries and Wildlife, Michigan State Univ., East Lansing 48824.* *Accepted 13 Jan. 1975.*

Mourning Doves breeding in an unusual habitat: the coastal spruce forest. —Mourning Doves *Zenaida macroura* frequent rather open or brushy areas, including such man-modified habitats as suburbs and farmlands (Aldrich and Duvall, Condor 60:108–128. 1958). Aldrich and Duvall (op. cit.) characterize the Mourning Dove as "a widespread species in North America except in the boreal region". Numbers of this species have recently increased markedly in the northeastern U.S. and adjacent Canada (Fobes, Maine Field Nat. 15:30–45, 1959). However, while these birds often nest in conifers (e.g., Harris et al., Am. Midl. Nat. 69:150–172, 1963; Caldwell, J. Wildl. Manage. 28:732–738, 1964), there has been no documentation that they forage in coniferous forests.

Since 1969 I have occasionally observed Mourning Doves during the breeding season on Hog Island (Todd Wildlife Sanctuary), Bremen, Lincoln Co., Maine, in a mature forest consisting primarily of red spruce (*Picea rubens*) with small numbers of white

spruce (*P. glauca*) and occasional white pine (*Pinus strobus*). These doves concentrated their activities in an area of several hectares that was nearly leveled by hurricanes in 1954 and that is now covered by the rotting debris of the old spruces, patches of young spruces up to 7 m in height, and clumps of hay-scented fern (*Dennstaedia punctilobula*), with occasional small open areas and scattered trees remaining from the old forest. Though I found no nest, the consistent presence there of doves in twos and their frequent vocalizations suggested that they were breeding.

In 1974 I observed 2 Mourning Doves together nearly daily in the mature spruce forest. They concentrated their activities about a tiny opening about 20 × 8 m, far smaller than the openings in the hurricane-devastated area. On 6 occasions I flushed foraging birds from the ground in or near this opening. The space contained exposed rock, reindeer lichen (*Rangifera* spp.), haircap moss (*Polytrichum commune*), spruce and pine needles and cones, and a sparse intermittent cover of short grass.

On 1 July I flushed these birds and a partially grown young dove from the edge of this opening. The young bird's tail feathers were less than one-half grown; when it flew it reached the lowest limbs of an adjacent spruce only with considerable difficulty, suggesting strongly that it had been fledged nearby. During the following week I observed the young bird twice more nearby with the probable parents.

The doves nesting in the largely undisturbed spruce forests on Hog Island probably originated from the small population of birds in the area of blown-down trees. If this supposition is correct, Mourning Doves have entered a new habitat by a 2-step process, the first being residence in an area (heavily damaged spruce forest) bearing several similarities to habitats typically occupied by this species (large open areas, brush), as well as novel characteristics (areas of young spruces, occasional large spruces, edges of spruce forest). The move into a dense spruce forest resulted in acceptance of vegetational characteristics not typically associated with Mourning Doves, though one might argue that their tendency to frequent the tiny opening represents a response to conditions typically frequented by them. This proposed pattern of establishment closely resembles the 2-step colonization of British farmland by Oystercatchers (*Haematopus ostralegus*) suggested by Heppleston (J. Anim. Ecol. 41:23–51, 1972).

Though Mourning Doves are strong fliers and might simply nest in the spruce forest and feed elsewhere, as one might predict from the observations of Harris et al. (op. cit.) and Caldwell (op. cit.), the frequency with which I observed them foraging about the nesting area suggests that these doves did much feeding within the forest itself. Only one field exists within 2 km of the site of observations (on the adjacent mainland), and I never observed doves there; further, I never saw doves crossing between the island and the mainland. Thus, they apparently foraged largely or entirely on the island.

The common birds of the intact spruce forest used by these doves (Black-throated Green Warbler, *Dendroica virens*; Blackburnian Warbler, *D. fusca*; Yellow-rumped Warbler, *D. coronata*; Dark-eyed Junco, *Junco hyemalis*; Golden-crowned Kinglet, *Regulus satrapa*; Red-breasted Nuthatch, *Sitta canadensis*) characteristically breed in such areas. None of the species typical of heavily disturbed forests in this vicinity (e.g., Yellowthroat, *Geothlypis trichas*; Song Sparrow, *Melospiza melodia*) breed in largely unbroken forests similar to those where the Mourning Doves were observed in 1974, which makes the presence of the doves in this spruce forest particularly noteworthy and suggests that openings of the size frequented by this pair of birds are usually inadequate to attract species typical of other habitats.

In the summers of 1971, 1972, and 1974, I continually saw and heard Mourning

Doves in a similar though somewhat younger and denser red spruce forest on Loud's Is., Bristol, 3 km to the south. The parallels between these activities and those that I have reported from Hog Is. suggest that the doves on Loud's Is. were breeding as well.

I made these observations while conducting other research sponsored by the National Science Foundation (GB-6071, GB-31005). The National Audubon Society kindly permitted me to work in the Todd Wildlife Sanctuary.—Douglass H. Morse, *Dept. of Zoology, Univ. of Maryland, College Park 20742.* *Accepted 18 Dec. 1974.*

Spring migration of Sandhill Cranes from Florida.—The behavior of Sandhill Cranes (*Grus canadensis*) during their spring departure from Florida was described by Williams (Auk 87:156–157, 1970) but little information has been published on the conditions associated with spring departure. During spring of 1972 and 1973, 2198 cranes were observed departing Paynes Prairie, Alachua Co., Florida. Migration was also noted during 1974 and 1975, but detailed records were not kept. Weather information was obtained from daily weather maps of the National Oceanic and Atmospheric Administration, Environmental Data Service, U.S. Department of Commerce, and the Federal Aviation Administration (facilities located 10 Km N Paynes Prairie).

Earliest observed departure was at 09:01 and the latest was 12:29 EST. Mean time of initiation of migration was 10:16 with 91% of the cranes leaving between 09:45 and 11:15. A majority of departures (84%) for the 2 springs studied, occurred during the first 12 days in March. The earliest date of observed departure was 18 February 1975; the latest was 9 birds seen leaving 7 April 1974.

Table 1 shows the mean weather conditions for 26 departure days and 8 days within migration period when no departures occurred. Rising barometric pressure, warm temperature, and southeasterly winds of about 18 km/hr are associated with spring departure. Such conditions occur after west to east passage of high pressure systems during early spring. This phenomenon and the associated winds were described by Bagg, et al. (Wilson Bull. 62:5–19, 1950) as being associated with northward bird migration. Southeasterly winds would be significant to cranes migrating from Florida because their breeding areas in Michigan, Wisconsin, and

Table 1

Spring Departure of Sandhill Cranes and Mean Weather Conditions*

	26 Days of Departure ± S.D.	Range	8 Days of No Departure ± S.D.	Range
Temperature (C°)	22 ± 1.68	12–26	20 ± 1.26	14–24
Barometric pressure (cm of mercury)	77.10 ± .41	76.33–77.64	76.84 ± .44	76.77–77.66
Wind direction (000–350°)	158 ± 54.28	050–220	(>158)212 ± 36.86 (<158)051 ± 36.86	020–290
Wind speed (km/hr)	17.79 ± 4.08	7.41–27.80	14.45 ± 6.39	5.56–27.80

* Based on 3 hourly readings between 09:50 and 11:50.

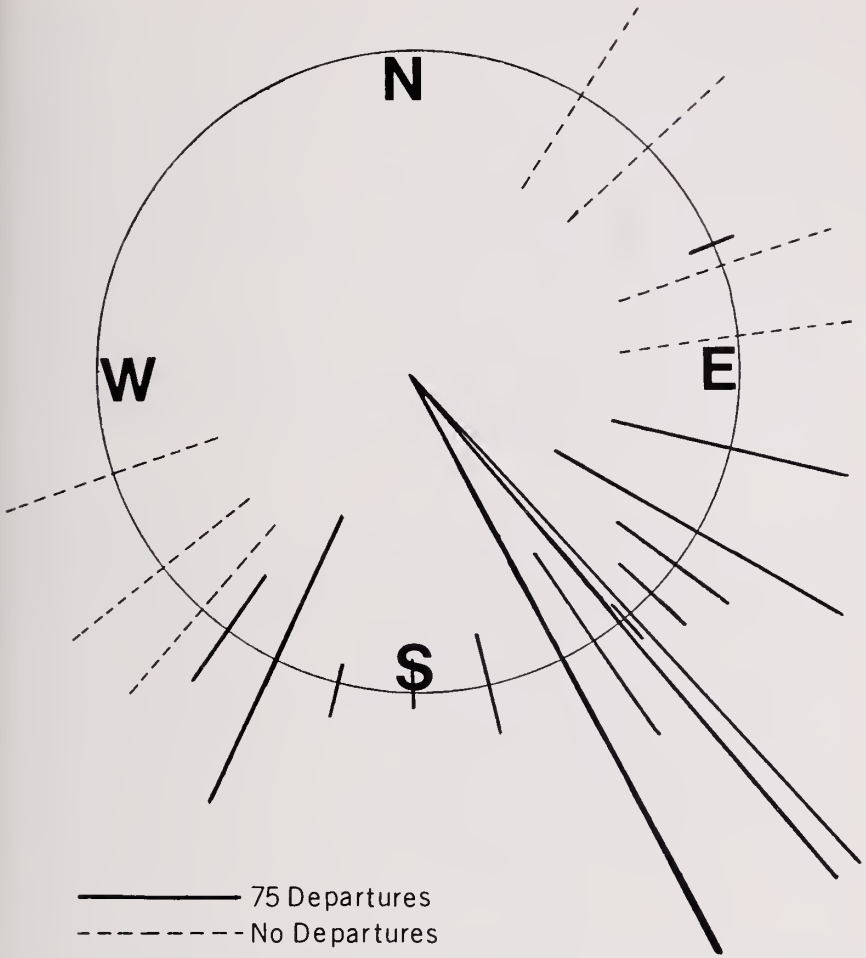

FIG. 1. Number of crane departures (length of line) and relative wind direction.

Minnesota (Williams and Phillips, Auk 89:541–548, 1972) are northwest of Florida. The influence of wind direction on departure is shown in Fig. 1. Although it does not appear in the table, clear skies appeared to be necessary for migration. On 13 March 1973, first departure occurred at 12:15 only after clear sky appeared through a previously complete overcast. On other days of complete overcast no departures occurred.

On several occasions migrating cranes passing over Paynes Prairie, at an estimated altitude of 800–1500 m, descended to approximately 500 m, called excitedly and circled over the northwest side of the prairie. Cranes from the prairie joined these birds and the merged flock gained altitude and disappeared on a northwesterly course. Such departures usually occurred between 12:00 and 13:00. The sight and sound

of these migrating cranes seemed to stimulate migration in remaining cranes. On 2 occasions, cranes were observed to join Wood Storks (*Mycteria americana*) flying over the prairie in a northerly direction.

The supposition by Bowman and Whitman (Auk 89:660, 1972) that cranes migrate simultaneously throughout the state is confirmed by these over-flying cranes. During 10 migration days in 1972 and 1973, 337 cranes were observed passing over Paynes Prairie, some as late as 14:30. Assuming 10:15 as a mean departure time, these cranes had been in the air for over 4 hours. A hypothetical ground speed of 80 km/hr would make the point of departure at about the known southern limit for Sandhill Cranes wintering in Florida (Lewis et al., *In* Management of Migratory Shore and Upland Game Birds in North America, G. C. Sanderson, ed., U. S. Fish and Wildlife Service, Washington, D.C., in press).

I am grateful to Lovett E. Williams, Jr. and James C. Lewis for reviewing this manuscript and offering many helpful suggestions. This study was in part a contribution of the Federal Aid to Wildlife Restoration Program, Florida Pittman-Robertson Project W-41.—Stephen A. Nesbitt, *Florida Game and Fresh Water Fish Commission, 4005 S. Main Street, Gainesville 32601.* *Accepted 20 Jan. 1975.*

Optical and gamma radiation measurements of the effects of chlorinated hydrocarbons on egg shells of Red-winged Blackbirds.—The relation between the thickness of egg shells of Red-winged Blackbirds (*Agelaius phoeniceus*) and the use of chlorinated hydrocarbons as insecticides was investigated by Fred J. Alsop (Ph.D. thesis, Univ. of Tennessee, 1972). He measured the thickness of each shell microscopically with an image splitting eyepiece allowing an accuracy of approximately 2.4 microns. He found that shells from eggs laid before 1940, before DDT was introduced, were thicker than egg shells laid in 1970 and 1971, and that eggs laid in these latter years in areas where chlorinated hydrocarbons are heavily used had thinner shells than those from other areas.

After completion of Alsop's study, an instrument was developed at the University of Tennessee to measure the density of very small sections of wood cores using gamma radiation from an iron-55 source (Woods and Lawhon, Forest Sci. 20:269–271, 1974). We decided to see if this radiation densitometer could be used to detect thinning and possibly other changes in eggshells due to insecticide use. Eggs collected by Alsop in 1970–71 in 2 areas were used. Hamilton County in southeastern Tennessee includes relatively little agricultural land, and insecticide use is light. Crittenden County, eastern Arkansas, is cotton country where insecticides are frequently dispersed from planes. Sixteen clutches had been collected from each county, 35 eggs from Hamilton and 33 from Crittenden. Samples of egg shell were prepared by cutting pieces about 1 cm square from the flattest part of the shell. Each piece was placed in the beam (circular, 1 mm diameter) of gamma radiation, and the amount of radiation transmitted from the source through the shell to the detector was measured for a period of 100 sec. The radiation transmitted through air alone was measured frequently for a similar interval to allow calculation of the fraction of radiation transmitted by each shell. The thickness of each piece of shell used in the radiation measurements was measured by the same optical apparatus used by Alsop; to facilitate doing this, the pieces were first placed in a weak solution of trypsin for 2 or 3 days until the membranes could be peeled away to leave only the shell.

Of the radiation entering a material, the fraction transmitted through it is an ex-

ponential function of the thickness and the absorption coefficient of the transmitting material (U. Fano, *in* Principles of Radiation Biology, A. Hollaender, ed. vol. 1, p. 103. 1954); i.e., the logarithm of the fraction transmitted is a linear function of the product of the thickness and the absorption coefficient.

Statistical tests were first performed separately on shell thickness measured optically and on radiation data (logarithm of the fraction transmitted). Eggs from Hamilton Co. had thicker shells than those from Crittenden Co. Using the data from all eggs, the difference in thickness was not significant at the 5% level, but when 3 eggs from Hamilton and 2 from Crittenden Co.—eggs with shell thickness at least 2 standard deviations removed from the mean of their respective groups—were eliminated from the data, the difference was significant at the 1% level. Similarly, eggs from Hamilton Co. transmitted less radiation than the others; using the measurements from all eggs, the difference was significant at the 5% level. The radiation technique, therefore, gave slightly better results in differentiating between the groups. Also, the radiation measurements had slightly smaller coefficients of variation indicating more consistency.

We also calculated linear regressions with the logarithm of the fraction of radiation transmitted being a function of the shell thickness. The 5 eggs mentioned in the preceding paragraph were omitted from these calculations. Regression coefficients from the data for each county were not significantly different, but were in fact almost identical. This indicates that the samples differed only in shell thickness, and that chlorinated hydrocarbons affect only this characteristic and have no effect on the chemical and physical characteristics determining the absorption coefficient. A single regression was calculated from the data of both counties combined, and the resulting equation is:

$$(\log \text{ of fraction transmitted}) = -0.880 - (0.0199/\text{micron})\ (\text{thickness in microns}).$$

The regression coefficient is very significantly different from zero.

In conclusion, the effect of chlorinated hydrocarbons on egg shells is primarily if not entirely on their thickness, and radiation absorption methods are only slightly superior to optical methods in measuring this effect. The optical methods are much faster and cheaper.—James T. Tanner and Wayne W. Tolbert, *Graduate Program in Ecology, Univ. of Tennessee, Knoxville 37916.* *Accepted 24 Jan. 1975.*

Two female Wood Ducks call brood from nest box.—At the Duck Creek Wildlife Area, Puxico, Missouri, on 5 June and again on 12 June, 1973 I found 2 female Wood Ducks (*Aix sponsa*) incubating a clutch of 21 eggs. The number of eggs in the clutch and the rate of egg laying suggested that both females contributed to the clutch simultaneously.

One female (756-00205) was banded as a nesting female in 1971. Her 1971 nest and her subsequent nest in 1972 were both dump nests. Thus she was at least 3 years old and tolerant of intrusion by other females into her nesting box when she nested in 1973. The second female (756-00296) was identified by a web tag as having hatched in a dump nest in 1970; she was not found nesting on Duck Creek prior to 1973. No earlier association of the 2 females is known.

On 13 June 1973 at 06:48 (CDT) one female flushed from the nest box then containing 13 dry ducklings, 3 dead ducklings, and 2 eggs with dead embryos; 3 other eggs were missing. At 07:11 a pair of Wood Ducks flew into the area, the female landed in the mouth of the nest box and entered, the male kept flying and left the

area immediately. At 07:18 the first female, which had remained near the box on the water, flew up to the nest box and entered. Between then and 08:18, when the young started jumping from the box, the 2 females were heard calling to the young and alternately flew down to the water and up into the box. Both females were on the water below the box as the brood exited. When all the ducklings had left the nest box, the 2 females swam away with the brood. One female had most of the brood; the second female had at least one duckling with her and swam approximately 10 m behind the first female.

Simultaneous occupation of a nest box by 2 female Wood Ducks has been observed by Bellrose (Auk 60:446–447, 1943) and Fuller and Bolen (Wilson Bull. 75:94–95, 1963), but neither reported observation of both females calling the brood from the nest. In Illinois, one female left the nest box with 26 ducklings and the second female left with 2 ducklings a day later (Bellrose op. cit.). In Vermont, one female was on the nest and a second female was on the water near the nest box when hatching occurred, but the exodus of the brood was not observed (Fuller and Bolen op. cit.).—Richard L. Clawson, *School of Forestry, Fisheries and Wildlife, Univ. of Missouri-Columbia, Gaylord Memorial Laboratory, Puxico, MO 63960.* *Accepted 23 Jan. 1975.*

ORNITHOLOGICAL NEWS

In the review (Wilson Bull. 87:292–296 1975) of "Productivity, Population Dynamics and Systematics of Granivorous Birds," edited by S. C. Kendeigh and J. Pinowski, published by the Institute of Ecology near Warsaw, Poland, it was stated that the book was available from Dr. Pinowski in Poland. It would probably be more convenient and faster for persons in this and other western countries to order the book from Dr. S. C. Kendeigh (Vivarium, Wright and Healey Streets, Champaign, IL 61820). The price is $13.00 plus 60¢ for postage and handling.

Plan now to attend the Wilson Ornithological Society's fifty-seventh annual meeting at Cornell University, Ithaca, New York, 3–6 June 1976.

A court fight by the Mississippi Wildlife Federation and the National Wildlife Federation to stop the construction of U.S. Interstate 10 through the breeding area of the Mississippi Sandhill Crane was lost last month following testimony by a U.S. Fish and Wildlife Service biologist that the construction would not adversely affect the cranes. An appeal of the decision is anticipated.

"Even-aged management"—clear-cutting—is now the recommended management practice for most of our southern National Forests. Recently it was announced that forests on some of our southern National Wildlife Refuges are also being subjected to this controversial practice!

ORNITHOLOGICAL LITERATURE

Avian Speciation in Tropical South America. By Jürgen Haffer. Publications of the Nuttall Ornithological Club, No. 14, Cambridge, Mass., 1974: viii + 390 pp., many figures, tables, maps. $19.00. (Obtainable from the Nuttall Ornithological Club, c/o Museum of Comparative Zoology, Harvard Univ., Cambridge, MA 02138)—It is a rare individual that becomes an international leader in his chosen field, but it is an even rarer one that does it in his spare time. Jürgen Haffer is a petroleum geologist. For a period of 8 years between 1957 and 1967 he was based in Colombia, and for much of this time he lived in the steamy jungles of the lower Atrato Basin and Gulf of Urabá region. It was during this period when, following a natural affinity for birds, he became interested in speciation, his attention having been attracted by several prominent cases of hybridization in a region containing the contact zones of many related Central and South American forms. He began to publish on the birds of the Urabá region in 1959. As his experience with the Neotropical avifauna increased, he began to perceive the remarkably consistent distributional patterns that provide the empirical substrate for the present volume. The first expositions of his views on the role of cyclical climatic changes in the speciation process were in landmark papers that appeared in 1967 and 1969. His book expands on the material contained in those papers, and offers a wealth of additional supportive evidence, both geological and biological.

Haffer's thesis is that a high proportion of the species, semispecies, and races of Neotropical forest birds differentiated during late Pleistocene times in a set of isolated pockets of high rainfall that supported humid evergreen forest when most of the continent was comparatively arid and covered with non-forest vegetation (savannahs, thorn scrub, etc.). There is extensive physical and geological evidence behind the contention that South America experienced a series of alternations between relatively wet and dry conditions during the Pleistocene. The stratigraphy, palynology, and glaciology of the continent all lead to similar conclusions. A precise chronology has yet to be established, as have the correlations with phases of glacial advance and retreat in the Northern Hemisphere. But these insufficiencies in our knowledge do not in the least mitigate the force of Haffer's arguments which depend simply on the historical fact of climatic reverses. Others before Haffer (especially Moreau and Keast) realized that unstable Pleistocene climates played an important role in the speciation of birds and other taxonomic groups in the tropics, but it had not been previously appreciated that Pleistocene events had a truly overwhelming influence on today's taxonomic relationships and distributional patterns.

The book opens with a series of concise background chapters on the Ecological Geography of Tropical South America, the History of Ornithological Exploration, Important Collecting Stations, and the Composition of the Neotropical Avifauna. The heart of the work, and of Haffer's own contribution begins with Chapter 9 on Distribution Patterns and Population Structure of Neotropical Forest Birds. Here he marshalls the zoological evidence for the existence of Pleistocene forest refugia: centers of endemism, the distribution of the allospecies of superspecies groups and the location of hybrid zones and zones of secondary contact. Remarkably consistent distributional patterns appear in diverse bird families with widely different habits and trophic status: frugivorous guans, cotingas and manakins; omnivorous trumpeters and toucans; and insectivorous jacamars, woodpeckers, and icterids. The separate lines of evidence all point to a limited number of centers of differentiation that are

interpreted to have been disconnected outposts of humid forest during the recurrent dry interludes of the Pleistocene. Some 15 refugia are postulated from the biological data: 3 in Central America, 3 in trans-Andean Northwestern South America, and 9 in cis-Andean South America. Seven or 8 of these can be considered major. Ancillary evidence from other taxonomic groups, so far as is available, points to very much the same set of refugia. More or less detailed analyses have been published of lizards (*Anolis chrysolepis*), *Heliconius* butterflies, the *Drosophila willistoni* and *paulistorum* complexes, arboviruses, tapirs, certain monkeys, and plant families. The inferred positions of major refugia are the same in every instance, although the number and identity of suggested minor refugia vary from case to case. Only the largest refugia appear to have been significant for mammals, while plants seem to have survived in areas too small to show up in the bird data. This is precisely what we would expect if survival in forest islands were a function of the size of the contained populations.

Two short chapters discuss the biogeography of the tropical non-forest and montane avifaunas of South America. Under today's relatively humid conditions, non-forest vegetation is found in 2 major regions to the north and south of the forested central Amazon basin. The wide separation would suggest a high degree of differentiation in their respective avifaunas; yet this is strikingly not the case. Most of the genera, and even many of the species of the Caribbean coastal deciduous forests and xeric scrub are common to similar formations in southeastern Brazil, the cerrado, and caatinga, adding strength to Haffer's contention that the 2 regions were connected by broad corridors during a relatively recent dry interval. This interpretation is further supported by the existence today of numerous undifferentiated non-forest forms which occur in the many isolated savannah and scrub enclaves that are scattered through the forest of the Guianas and eastern Brazil. As for the montane faunas, a repeated lowering and raising of elevational vegetation zones can be presumed to have successively opened and closed corridors of access, both between sectors of the Andes that are transected by deep arid gorges, and between the Andes and isolated mountain masses in southern Venezuela, the Guianas, and southeastern Brazil.

An important chapter on the Geologic and Climatic History of Tropical South America will be of special interest to biologists, because it is here that Haffer's expertise and perspective as a geologist come forward. In the space of 22 pages he discusses such topics as the breakaway of South America from Pangea in the Cretaceous, the geologic structure of South America, the formation of the Amazon basin, the Andean orogeny, and the formation of the Middle American isthmus. The presentation is admirably concise and informative, synthesizing a vast amount of literature and knowledgeable first hand experience.

The final section of the book, consisting of nearly half its length, lays out a detailed systematic treatment of 2 autochthonous South American bird families, the toucans and jacamars. Haffer's 2-fold intention here was to revise the somewhat muddled taxonomy of these groups while presenting further, more detailed evidence in support of the thesis he expounds in the first part of the book, incidentally demonstrating how the recognition of refuge areas can help in analyzing phyletic relationships. While exemplary as a modern study in systematics by its extensive use of sonograms and ecological information, this section will be of less interest to the non-systematist who, for his $19, may feel that this is too heavy a dose of specialized material.

The major conclusions of Haffer's work lead to new insights into the stubborn problems of tropical diversity. Tropical regions share a unique geographical property:

climatic symmetry about the equator. With the advent of a dry period, the continuous evergreen forest breaks up centrifugally into peripherally isolated refugia. Undoubtedly, many local extinctions occurred in these refugia, but their very number provided a redundancy which assured that few species lines vanished altogether. A large number of effective refugia allows speciation to run ahead of extinction. Quite a different situation prevailed at temperate latitudes. Climates varied along a steep gradient. Populations could retreat into refugia by moving in only one direction—towards the equator. Necessarily the number of refugia was small. Instead of the 7 or 8 that existed in the Neotropical region, North America offered only 2 major refugia, the Florida peninsula and Texas-Mexico. Consequently, instead of having many superspecies groups that are made up of 5 or 6 members, North America has superspecies that normally contain only 2 members, e.g., the buntings, orioles, bluebirds, grosbeaks, meadowlarks, tanagers, etc.

Haffer's work completely destroys the notion of tropical faunas as "old" and "stable." Rather, they appear to be young and dynamic. This holds even for such allegedly conservative non-passerine groups as parrots, jacamars, and toucans. Ironically, it is beginning to look as if the climatic and vegetational *instability* of the tropics is a major cause of high tropical diversity.—John Terborgh

Autumn of the Eagle. By George Laycock. Charles Scribner's Sons, New York, 1973: 239 pp., photographs and maps. $6.95.—This is an informal but engaging account of the life of the Bald Eagle, and its decline and threatened extinction at the hands of mankind. In addition to accounts of its life and habits, there are numerous discussions of individuals and organizations who have been prominent in the study, destruction, and preservation of our national bird.—R. J. R.

Song of the North Wind: A Story of the Snow Goose. By Paul A. Johnsgard. Anchor/Doubleday, Garden City, New York, 1974: 150 pp., B & W Illus. by Paul Geraghty, 27 photos. $5.95.—The author resolved "to write a story that not only might be biologically accurate, but which might also bring into sharp focus the contrasting visions of our natural resources as seen by aboriginal North Americans and by our policy making bureaucrats in Washington, as well as establish parallels in the attitudes of whites toward both our wildlife and the Indians." In a highly readable, popular fashion, Johnsgard has succeeded well in accomplishing his goals.

After a preface in which the author recounts his boyhood experiences with Snow Geese in North Dakota, the book shifts to a discussion of the colonization of North America by aboriginal people. Hypothetical encounters by these people with North American wildlife are included. The remainder of the book follows a year in the life of Snow Geese, principally those from Southampton Island, starting and ending with geese on their tundra breeding ground. Recent research on the Snow Goose is summarized and a great deal of information on goose biology is interestingly presented. The plight of geese in the face of terrific pressure both from hunting and through environmental destruction is well pointed out. Twenty-three Indian and Eskimo stories, ceremonies, and myths, interesting enough on their own, are augmented by the 17

impressionistic pen and ink drawings of Paul Geraghty. The 27 photos at the rear of the book are of little value. Had they been placed near appropriate discussions, about half of them would have enhanced the book.

Overall, this is a well done popular account of Snow Geese. It will be of special interest to anyone who marvels at the sight of geese overhead.—Lewis W. Oring.

Francis Lee Jaques/ Artist of the Wilderness World. By Florence Page Jaques. Foreword by Roger Tory Peterson. Doubleday & Co., Garden City, N.Y., 1973: xxi + 370 pp., 64 col. paintings and dioramas, 100 drawings. $25.00.—We have here a handsome book on the life and works of one of America's finest wildlife artists, Francis Lee Jaques. This humble, gentle man, of exceptional talents, brought the museum diorama to a fine art form. Over the years, millions of people have stared through huge plate glass windows and momentarily lost themselves in his wilderness vignettes. Few museum visitors ever knew the name of the man who created these glorious backgrounds of limitless prairies, dazzling sandy beaches, fog rolling in from Arctic seas, sun-baked African plains, or an English countryside in May. The great Whitney Bird Hall in The American Museum of Natural History, with all of its backgrounds painted by Jaques, has no plaque or marker giving credit to his work.

Jaques' museum background painting, however, represents but one approach to his artistic world. His many oil paintings are tops in their field, and I believe his pen and ink scratch board drawings have never been surpassed.

Luckily, Florence Page Jaques, who survived her husband by three years, was able to gather her memories and write a most touching and excellent biographical essay on their young days and married life together. In her early eighties, but with a keen mind, she also was able to select some of the most representative examples of her husband's art for publication in this book.

The biographical essay is followed by a large collection of paintings, mostly color reproductions of oils. Three appraisals of Jaques as an artist are then followed by many pencil drawings of animals. Next come carefully chosen excerpts from the Jaques' 6 popular books. An appendix contains Jaques' short journal of his trip to the Peruvian islands, Louis H. Westcott's description of the artist's unique home model railroad system, and "A buffalo hunt" by Ephraim Jaques, the artist's father, which was published in the magazine FOREST AND STREAM in 1900. These varying selections and approaches may sound fragmentary as I describe them, but they serve, each in its way, to give special substance to the Jaques story. The different sections of the book stand on their own, and can be read as separate entities.

Going over the artwork carefully, I found few title errors. The pencil drawing titles of wolverine and martin are reversed, and the leaping dolphins are common dolphin, not bottle-nosed. The scratch board drawing of swimming loons (p. 33) is tilted out of position with the drawing reversed, as the characteristic F.L.J. signature testifies. With so many top paintings to choose from, I was disappointed to see two oils of Wood Ducks, both of them rather lifeless, over-stylized, and very similar. The double-page illustrations for William O. Douglas' *My Wilderness* (pp. 102–107) are untitled and thus confusing. I found it hard to distinguish whether some of the drawings were one-page reproductions or meant to stretch across two pages.

Lee Jaques' love and understanding of that almost extinct species, the steam locomotive, was truly marvelous. A few oils reproduced in the book testify to his love affair with trains. As a kid in New York, I often went to the Kennedy Galleries, where many of his

finest paintings were on show. I marveled that a man could be so diversified in his talent as to paint trains and birds with the same devotion.

Lee Jaques' black and white scratch board drawings have seldom been equalled in the field of natural history. His composition, placement, and simplicity of dark shapes on a white field and vice versa never cease to hold me spellbound. How few well-placed lines a skilled technician really needs to convey his message to the viewer! I would like to have seen more of these drawings reproduced.

Glancing over the 50-odd oil paintings that are shown, I was most impressed with those that depict a mammal or bird in relation to vast expanses of air, water, clouds, or just space. The pen and inks can take you into a dark, bushy corner and show you a hiding snowshoe rabbit, but the oils really turn your mind completely free to explore the horizon. To me, 6 exceptionally fine paintings are "Morrisey and Ivory Gull" (p. 132), "Red Fox on Alaskan Peninsula" (p. 140), "Road After Rain" (p. 158), "Pronghorn Antelope" (p. 214), and "Passing of the Old West" (p. 224). The last has an N. C. Wyeth mood and Peter Scott formations of geese, but the final result is strictly Jaques, and a deeply moving picture, indeed.

Florence Page Jaques' text, both the biographical essay and the excerpts from the 6 books provide delightful reading. She has great warmth, a gentle sense of humor, and excellent power of description. Writing about personalities, friends, and acquaintances, she minces no words in telling whom she was or was not fond of, and why.

In reviewing this book on the life and work of Francis Lee Jaques, I am compelled to compare it to *Louis Agassiz Fuertes and the Singular Beauty of Birds*, edited by Frederick George Marcham (Harper & Row, 1971). Fuertes, 13 years Jaques' senior, had a brilliant life, cut short while crossing a railroad track in 1927. Fuertes was the master of bird portraiture in this country since John James Audubon, and he is still the hero of almost every bird painter. His was not the genius of composition or background, but of the eye that caught the exact shape, size, and placement of nostril, bill, and gape, and directed the brush strokes that recreated the living bird. We still stand in awe of his chickadees and gyrfalcons. The art work chosen for this coffee-table extravaganza does not, in any way show the full range of Fuertes' talents. In his desire to reproduce unfamiliar paintings, the editor used much second class work, often incorrectly titled. The greatest faults, however, are the enlargement of several tiny rough watercolor sketches to full page size, and the printing of a crude drawing of a screech owl with no mention in the caption that it was done when Fuertes was a child.

No crimes of this calibre have been perpetrated in this fine volume of Jaques. Both art and reading matter are well chosen and in excellent taste.—John Henry Dick

Eagle Days. A Study of African Eagles at the Nest. By Peter Steyn. Purnell Library Service, New York, 1973: xviii + 158 pp., 147 photographs (22 in color). $24.55. —Surely the great African eagles are the finest collection of raptorial birds in the world, and the author's handsome photographs bring us an unparalleled nest-side panorama to which no words can do justice. The many large plates of more than 10 species portray not only the eagles and their nests, but bring such a sense of intimacy that the reader feels himself a participant of the scene, in which bird, nest, tree, surroundings, and more distant terrain are grasped in a breath-takingly vivid view. The text is narrative, always entertainingly and often beautifully written, an account of Peter Steyn's personal experience with eagles beginning as a young lad on the slopes of Table Mountain above Cape

Town viewing through mist-shrouded cliffs the magnificent Verreaux's Eagle. Within a few years the author's love for the eagles was becoming recognized as his photographs and accounts of eagles began to appear, particularly in *Bokmakierie* and *Ostrich*. This book fills in all the gaps in his series of scientific papers, and to one familiar with the latter, it is a delight to now locate and place in both time and location the various nest-sites and eagle experiences, and all the while gaining an added breadth to his view of this unique ornithological scene.

Major accounts are given of 10 African eagles, along with some comments and experiences with others, as well as a Golden Eagle safari in Scotland with Leslie Brown, with an Eric Hosking photograph.

All the chapters are excellent reading, but those on the Snake Eagles, Tawny, and African Hawk-Eagle are much more complete. I have the feeling that the chapter on the Black Eagle has less information simply because his close friend and associate Valerie Gargett is making already world-famous studies upon this species, and in like manner, the Fish Eagle and Crowned Eagle chapters may not be as complete in deference to the work of his friend and colleague, Leslie Brown (who has provided a delightful Foreword. . . I shall never forget MacCrimmon!). The average reader will not have read Mr. Steyn's accounts of the "Brown Snake" and "Black-breasted Snake" in *Ostrich*, and to him the accounts of these cobra-eating eagles will seem incredible. How does the eagle avoid fatal poisoning in capturing the black-necked spitting cobra whose second-splitting jet of poison aims straight at the eyes . . . is the nictitating membrane sufficient? And the almost ludicrous feat of a Black-breasted Snake Eagle in full flight swallowing a snake head first, the snake being inched forward by the eagle's feet in conveyor-belt fashion . . . and then being pulled forth and again swallowed . . . all in all 6 times! Incidentally, a cobra is swallowed at 30 cm a minute. And to those of us who have felt safe tramping the Matopos hills in the cold months, let is be known that the snake eagles bring in a fine array of cobras, boomslangs, and puff adders to their nests.

All in all, this is about the finest book on the "hook-bills" that I have ever read, and the color plate reproduction is simply superb. My one regret is that the latter could easily have shown more of the late-nestling juvenal plumages; . . . the fledgling Verreaux's Eagle is a beautiful warm brown and brick red, in startling contrast to the somber black and white of its "Black Eagle" parents.—Walter R. Spofford.

Swans of the World. By Sylvia Bruce Wilmore. Taplinger Publishing Co., Inc., New York, 1974: 229 pp., eight half-tone plates, eleven maps, numerous line drawings by the author. $9.95.—This book, by an English cygniphile, is the second book-length summary on swans to appear in the last 2 years. The other, *The Swans*, published in 1972 by the staff of the Wildfowl Trust, is so similar to it that comparisons are inevitable.

Mrs. Wilmore has generally organized her book into a series of species accounts, plus 4 introductory or comparative chapters, whereas the Wildfowl Trust's book is entirely comparative in organization. For the lay reader, who might wish to readily extract all the available information on, say, the Mute Swan, this organization does have considerable appeal. Additionally, the species accounts are well-written and relatively comprehensive. There can be no doubt that Mrs. Wilmore has relied extensively on information available in *The Swans*, although a substantial number of her literature citations did not appear in that book. Regrettably, there are no in-text references to the literature used, and many of the references in the bibliography are either inaccurate or incomplete. Where in-text

references do occur (as on p. 37), these are not to be found in the bibliography. The line drawings, although adequate, cannot compare with the quality of the corresponding ones in *The Swans*. There are some errors of fact that no doubt result from the presumed non-scientist background of the author, such as the descriptions of the bone structure of the wing, the mechanism of feathering of the primaries during flight, and the functional significance of the V-formation of waterfowl in migration. There are other minor annoyances, such as the misuse of the term "mortality" in the accounts of the Black and Black-necked swans, the confusion of Whistling Swans for Trumpeter Swans as the breeding birds on the Clarence Rhode National Wildlife Range, and the use of outdated information on the Mute Swan population in North America.

All told, in its content and accuracy, the book is a compromise between such potboiler titles as *The World of the Swan* and the comprehensive expertise of *The Swans*. Thus the bird enthusiast who buys books primarily for their readability rather than as an effort to build a reference library may well wish to invest in *Swans of the World*. For one interested in the latter, the extra cost ($5 more) of *The Swans* would be the better choice.—Paul A. Johnsgard.

Parrots of the World. By Joseph M. Forshaw, illus. by William T. Cooper. Doubleday and Co., Inc., Garden City, New York, 1974: 584 pp., 158 color plates with caption figs., 344 range maps, 11 numbered text figs., 3 tables. $65.00.—No birds surpass the psittacines in being appropriate for a 19th century-style monograph, and no bird book produced in recent years equals "Parrots of the World" in copying the extravagant format characteristic of this bygone era. The book measures $11 \times 15\frac{1}{2} \times 2\frac{1}{2}$ inches, weighs over 10 pounds, and includes color paintings of almost 500 parrots.

Species accounts for all Recent parrots, including those known only from bones, occupy over 90% of the pages. These are divided into 3 "distributions," Pacific, Afro-Asian, and South American. Within each distribution the accounts are arranged in a sequence similar to that of Peters (1937, Check-list of Birds of the World, vol. 3, Harvard Univ. Press, Cambridge). Brief introductions to each distribution include analyses of its parrot fauna and a large map showing political areas. The 344 accounts are each about 2 to 3 pages long. They include brief species descriptions, information on distribution (and a range map), descriptions, and measurements of all subspecies, and general notes on natural history including calls, nesting, and eggs.

Preceding the species accounts are a foreword by Dean Amadon, and sections on fossils, classification, and natural history of the entire order. Reference to Brodkorb (1971, Bull. Florida State Mus., vol 15, no. 4) would improve the brief section on fossils. Forshaw clearly states that he is not a taxonomist, but still proposes a classification: it differs only in minor ways from that of Peters (*ibid.*), who recognized 1 family and 6 subfamilies. Forshaw proposes 3 families, the Loriidae, Cacatuidae, and Psitttacidae. The first 2 are the same in constituency as 2 of Peters' subfamilies. The third of Forshaw's families includes as subfamilies the remaining 4 subfamilies of Peters, the Strigopinae, Nestorinae, Micropsittacinae, and Psittacinae. I was disappointed to find no reference to the fairly recent and innovative classification of parrots proposed by Hans von Boetticher ("Papageien." Die Neue Brehm-Bücherei, Heft 228, 1959). All other recent attempts at classifying the order seem to be included in the brief analysis.

The section on physical attributes includes 4 full-page figures. With the surfeit of space provided, additional features of the skeleton could have been labeled with no

crowding. For example, the toes are not numbered, and only abbreviated names are given for the 2 distal leg bones. Furthermore, certain wing bones distal to the radius and ulna are both incorrectly drawn and either labeled wrong or not at all. Mention of the considerable, and as yet unexplained, variation in furcular structure of parrots, for which several references exist, should have been included.

Forshaw's fascination with parrots goes back to his youth, and he has amassed extensive experience with a large number of species both in the field and the aviary. He has traveled extensively in Australia to observe wild parrots, and has visited Asia and the Americas for the same purpose. Related to this he has been most successful in bringing together the profuse and diffuse parrot literature published by aviculturists. His references cited take up 7 pages in small type.

The full page color plates are generally excellent. Particular attention has been given to the backgrounds and the results are most successful. My only general criticism is that for some of the species certain dark colors seem too dark. Short, in his review (Auk 76: 850–852, 1974), levied a similar complaint after examining several copies of the book. Each illustration is based on a specimen whose registration number is listed under the caption figures. These figures are the only direct references to the plates, but I find this system adequate.

My major complaint with the book is not with the contents, which generally are first-rate, but with the format. Unfortunately I find I must parrot certain of my criticisms of Forshaw's other recent work "Australian Parrots" (Wilson Bull. 83:107–108, 1971). The book is too big because of much wasted space. The margins are far too wide, and several maps and drawings could be much smaller with no loss of detail. The book could easily be 3 inches shorter. A related problem seems to be the binding. Short (*ibid.*) wondered if the covers (¼" thick) were too heavy to remain attached. On the copy I received, the front cover broke free of the pages when the review editor first opened the book. Certainly a smaller book would reduce several of these problems. Furthermore, the reduced size might have decreased the price, and thus put the book more within the means of the wide audience for which it was intended.—Glen E. Woolfenden

Check-list of Japanese Birds. Fifth and Revised Edition. The Ornithological Society of Japan. Gakken Co., Ltd., Tokyo. 1974. viii + 364 pp. in English; x + 120 pp. in Japanese. Bound separately; boxed together. $29.00. Available through International Division, Gakken Co. Ltd., 4–40–5. Kami-ikedai, Ohta-ku, Tokyo 145 Japan.—The area covered includes Japan proper, the southern Kuriles, the Ryukyus, the Bonins, and the Volcano Islands. A map of this region is found on the inside cover. The 490 species on the regular list are arranged in the order of Peters' "Check-list of Birds of the World." Species accounts in the English version include scientific, English, and Japanese names, reference to the original description, range, status in Japan, and habitat. Under each subspecies, reference to original description, range, and locality records are given. Indices to Japanese and scientific names, a list of synonyms and invalid names, and a list of species and subspecies "of uncertain records" complete the volume. References to original descriptions and species accounts are omitted from the Japanese version.

Approximately one-fourth of the species included are extinct, very rare, or of casual occurrence, and there is much inconsistency in the way in which the status of these birds is described. Species which have been found but once in Japan are variously listed as "accidental," "accidental straggler," "rare accidental," "rare straggler," or

"straggler." The terms "casual," "casual straggler," "occasional straggler," "rare casual," and "vagrant" are also used for rarities. It would be helpful to users of future editions if the person responsible for correcting the English would define such terms and see that they were used consistently.

Aside from this, there is little to criticize in this well planned and printed work. I found few errors (the name of Miyaki Island is omitted for the map in the English version) and was pleased to find documentation for a high proportion of the rarities. It is a concise and usable source of information on the distribution, status, and habitats of Japanese birds.—Robert W. Storer.

Birds of Western North America. Nonpasserines. Paintings by Kenneth L. Carlson; text by Laurence C. Binford. Macmillan Publishing Co., N. Y., and Collins Macmillan, London, 1974: 223 pp., 50 color plates, cloth, $25.00.—This book contains an 8-page introduction on the "hows," "whys," "wheres," and so on, of being a "birder." Then follow the plates with a page of text about each and an index which has entries for the birds and much of the vegetation shown with them. The page facing each plate is blank, except for a caption, and the backs of the plates are blank; all these are counted as numbered pages, thus giving considerable paging to 50 color plates plus brief commentary.

The text is chatty and informal, yet it contains much interesting biological information. The printing of the color plates is excellent. The species shown are western (including Pacific), there being both land and water birds, in size from hummingbirds to the California Condor.

In addition to this book, this reviewer also has recently looked at excellent reproductions of the work of several other illustrators who specialize in birds. A general impression gotten from this experience is one of too much sameness—as though each painter had kept an eye on the others so that their respective end results seem more alike than any constraints of subject matter require. Apparently another limiting factor is that most illustrators, and also the public in general, are so conditioned to visualizing birds as portrayed in field guides that arbitrarily maintaining the local color of feathering and soft parts seems to be the prime criterion of what currently is acceptable (and saleable?).

In the present book the birds are on white paper, with no background that might modify the local coloration of birds in the foreground, and essentially no perspective. Some of the birds are too flat, in this respect having only a very slight resemblance to figures on Japanese prints. The immediate surroundings of the birds are good, but occasionally a bit too obviously contrived; for example, the arrangement of vegetation around a white bird (Ross' Goose) to separate it from the white background. The constraint of maintaining local color inhibits logical opportunities to modify it even slightly so as to separate planes—an obvious need when one wing is behind the other (California Condor plate). The Green Kingfisher plate is rather innovative, showing the bird capturing a fish beneath the surface of the water. Yet the bird appears as it would in air: perfectly dry, all feathering in perfect arrangement, eye with highlight unmodified by aquatic environment.

Allowing for the conventions used in maintaining what some would term true-to-life colors, this reviewer rates about three-fifths of the plates as excellent to good, most of the others as of lesser quality, and a few as poor (usually for unsatisfactory anatomy). The whole production is moderately lavish and its main market probably is among affluent birders.—Ralph S. Palmer.

Systematics and Evolution of the Gruiformes (Class Aves). 3. Phylogeny of the Suborder Grues. By Joel Cracraft. Bull., Art. 1, Am. Mus. Nat. Hist. 151(1), 1973:127pp., 51 figs., 49 tables. Paper cover. $4.75. Available from the Librarian, American Museum of Natural History, New York, New York 10024.—This work is Cracraft's third contribution in a comprehensive review of the fossil Gruiformes and includes a summary of his earlier revisions of the Geranoididae and the Bathornithidae. The monograph is divided into 6 major sections with the bulk of it (82 p) devoted to morphology and systematics. There are many excellent stereophotographs, but they are not to any exact scale and there is no consistent orientation of individual bones. The descriptions are detailed, but are sometimes hard to follow. Comparisons are facilitated by several tables comparing morphological features of various genera.

The work deals with the phylogeny of the suborder Grues which Cracraft divided into 2 infraorders, the Ralli and the Grui. Major taxonomic changes include: the placement of *Ibidopsis* in the Rallidae rather than in the Threskiornithidae (Ciconiiformes); the creation of a new family and superfamily, the Laornithidae and Laornithoidea, for Marsh's Cretaceous species *Laornis evardsianus;* the placement of *Gypsornis* in the Idiornithidae rather than in the Rallidae; and the Ergilornithidae are Gruiformes and do not share a close common ancestory with the Struthioniformes. Three new species are described within the Rallidae: *Palaeorallus brodkorbi, Quercyrallus quercy,* and *Palaeoaramides minutus;* and one within the Idiornithidae: *Idiornis gaillardi.*

Cracraft relies heavily on the features of the distal end of the tibiotarsus for making taxonomic decisions. This is largely beyond his control as it is the most commonly preserved element. However, I am not convinced that it has always led him to make correct systematic interpretations. I am especially dubious of the placement of the Laornithidae close to the Rallidae on the basis of general resemblance in this element. His restrictions of this study to extinct Tertiary genera seriously limits its "comprehensive scope." The inclusion of extinct Tertiary species of living genera would not have expanded it beyond reasonable limits, and would have necessitated comparisons with living genera, which are otherwise notably lacking.

There is a short section on morphological variability in fossil samples including examples drawn from the Idiornithdiae and the Bathornithidae, which provide useful information concerning the variability of these extinct families. Cracraft also provides an analysis of 4 Quaternary and/or Recent samples of rails. However, the formulation of generalities about variability in the avian skeleton might have been more useful if recent samples had been used.

In Cracraft's summary of the phylogeny of the infraorder Grui, he suggests that there are 2 distinct phyletic lines: one for the Geranoididae, Bathornithidae, and Idiornithidae, and one for the Gruidae, Psophiidae, Aramidae, Ergilornithidae, and Eogruidae. He suggests that the geranoidids are primitive gruiformes that gave rise to the idiornithids in Eurasia after they had dispersed across the North Atlantic intercontinental connection, and to the bathornithids in North America. The eogruids and ergilornithids share a close common ancestry, while the aramids and psophiids are especially close to each other, an arrangement that is difficult to reconcile with Olson's (Wilson Bull. 85:381, 1973) suggestion that the Psophiidae are close to the primitive Rallidae.

The section on evolutionary considerations contains a variety of rather unrelated topics including a discussion of convergence between ostriches (Struthionidae) and ergilornithids in the reduction and loss of the inner trochlea on the tarsometatarsus.

Rates of morphological change in bathornithids and the influence of Eocene-Oligocene climate on gruiform evolution are also discussed.

Cracraft devotes 2 pages to methods in classification. He argues that classifications should be based on derived characters in the sense of Hennig (Phylogenetic Systematics, Univ. Illinois Press, Urbana, 1966), and that classifications are best expressed in a dichotomous fashion. He gives an example of this type of arrangement for the Grues, which permits one to identify sister-groups in the classification. To do this he has to change the traditional rank of many gruiform taxa and he does not use it elsewhere in the work. In fact, there is little evidence of any special "cladistic approach" throughout the work, which tends to be very similar to other taxonomic reviews in paleontology.

There are a few typographical errors. *Palaeoaramides minutus* described as a new species on p. 30 is misspelled *P. minimus* in the table on p. 28, and *P. eximius* is misspelled *P. eximus* (p. 27–29). The characters on table 48 are not numbered, although they are referred to by number on p. 109.

This work comes into a virtual vacuum, as the only other large group of fossil birds to receive a taxonomic review in recent times is the penguins (Simpson, Bull. Am. Mus. Nat. Hist., 87, 1946). This, along with the extensive summary and numerous illustrations of fossil gruiformes, makes this publication a major contribution to the study of avian paleontology.—Larry D. Martin.

Birding from a Tractor Seat. By Charles T. Flugum. Privately printed (Box 30038, St. Paul, Minnesota), 1973: 435 pp., 20 black and white illustrations by Walter Breckenridge. $8.95.—This book is a compilation of 137 of Mr. Flugum's monthly columns which appeared in *Community Magazine*, published in Albert Lea, Minnesota. The short chapters take you through the seasons for the years 1952–1964. To quote the author (pp.333–34): "Birds apparently consider a tractor operator a part of the machine and do not associate the machine with danger. At any rate, a tractor seat is a good vantage point from which to see field birds at close range." Having found that a seat on a tractor was almost equivalent to being in a blind, the author was able to make close observations, particularly of field birds which some of us rarely see closely. The book is a pleasing combination of Mr. Flugum's personal experiences with birds and information about them from other sources. Interested in birds from early boyhood on the farm, Mr. Flugum has studied, read, talked to ornithologists, and attended meetings of ornithological societies. This results in his writing being very factual and with authoritative though brief discussions of some ornithological subjects. The nature of the book—a compilation of columns almost as printed—results naturally in some repetition of particular facts or subjects, but this does not detract from the charm.

It is nicely put together. Each essay is about 3 pages, the print is easy to read, typos are few, as are misspellings and grammatical errors. We may disagree with a few of his statements, but all in all it is very accurate.

There are a few charming illustrations by Walter Breckenridge, reprinted from elsewhere with credit, and a foreword by Howard Cleaves, who refers to the author as "an authentic dirt farmer." The author acknowledges many who encouraged him in his writing and helped him in other ways, from (alphabetically) A. A. Allen to Alexander Wetmore. He expresses appreciation to his mother, who encouraged his interest as a boy, and to his son who helped him edit his columns.

It may be nit-picking to point out that Turkeys are not in the pheasant family (p.187), that the Latin specific name should not be capitalized (p.226), that one of the chief values of the Arm and Hammer soda cards (p.331) was that the paintings were done by L. A. Fuertes (not mentioned), and that Longspurs are not "true larks" (p.72). These are very minor errors. An index would be helpful.

Put this book on your coffee table—pick it up and read a chapter or two at a time. One can dip into it at any time on any page with enjoyment.—Sally Hoyt Spofford.

EDITORIAL

For several years it has been the intended policy of the Wilson Bulletin editor not to allow literature citations that refer to "in-house" reports and other similar documents that are not available to the scientific community. Occasionally such citations have been published. In recent months the number of such citations in manuscripts submitted to the Wilson Bulletin has multiplied. This increase no doubt reflects government recognition of environmental problems and its bureaucratic response: environmental impact statements, detailed permit applications, management plans for endangered species, etc. Because some of these reports contain the raw data on which a manuscript is based, citation of them may be important. While I still do not encourage the practice, where necessary, such citations will be allowed if the author is willing to deposit a copy of the report (or the appropriate portion of it) in the Josselyn Van Tyne Memorial Library. Notice of the availability of the report will then be made in the Wilson Bulletin.

In addition to the above service, Wilson members should be aware that the Van Tyne Library also acts as a depository for English translations of foreign ornithological literature. Many translations are already available on request. If you have English translations of foreign literature that you are willing to share with the ornithological community, please send them to the Josselyn Van Tyne Memorial Library, The University of Michigan, Museum of Zoology, Ann Arbor, MI 48104.

Finally, the stock of many back issues of the Wilson Bulletin is low. If you have extra copies that are collecting dust, please consider donating them to the Wilson Society. Such donations are tax deductible and sale of the copies will facilitate the continued growth and services of the Van Tyne Library.

This issue of *The Wilson Bulletin* was published on 29 September 1975.

The Wilson Bulletin

Editor Jerome A. Jackson
Department of Zoology
P.O. Drawer Z
Mississippi State University
Mississippi State, MS 39762

Editorial Assistants Robert J. Esher
David F. Werschkul
Wayne C. Weber

Review Editor Robert Raikow
Department of Biology
University of Pittsburgh
Pittsburgh, PA 15213

Color Plate Editor William A. Lunk
865 North Wagner Road
Ann Arbor, MI 48103

Suggestions to Authors

See Wilson Bulletin, 87:144, 1975 for more detailed "Suggestions to Authors." Manuscripts intended for publication in *The Wilson Bulletin* should be submitted in duplicate, neatly typewritten, double-spaced, with at least 3 cm margins, and on one side only of good quality white paper. Do not submit xerographic copies that are made on slick, heavy paper. Tables should be typed on separate sheets, and should be narrow and deep rather than wide and shallow. Before preparing these, carefully consider whether the material is best presented in tabular form. Follow the AOU Check-list (Fifth Edition, 1957) and the 32nd Supplement (Auk, 90:411–419, 1973), insofar as scientific names of U.S. and Canadian birds are concerned. Summaries of major papers should be brief but quotable. Where fewer than 5 papers are cited, the citations may be included in the text. All citations in "General Notes" should be included in the text. Follow carefully the style used in this issue in listing the literature cited; otherwise, follow the "CBE Style Manual" (1972, AIBS). Photographs for illustrations should have good contrast and be on gloss paper. Submit prints unmounted and attach to each a brief but adequate legend. Do not write heavily on the backs of photographs. Diagrams and line drawings should be in black ink and their lettering large enough to permit reduction. Alterations in copy after the type has been set must be charged to the author.

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The Wilson Bulletin

PUBLISHED BY THE WILSON ORNITHOLOGICAL [illegible]

VOL. 87, NO. 4 DECEMBER 1975 PAGES 441–607

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THE WILSON BULLETIN

The official organ of the Wilson Ornithological Society, published quarterly, in March, June, September, and December. The subscription price, both in the United States and elsewhere, is $10.00 per year. Single copies, $2.50. Subscriptions, changes of address and claims for undelivered copies should be sent to the Treasurer. Most back issues of the *Bulletin* are available (at $2.50 each) and may be orderd from the Treasurer. Special prices will be quoted for quantity orders.

All articles and communications for publications, books and publications for reviews should be addressed to the Editor. Exchanges should be addressed to The Josselyn Van Tyne Memorial Library, Museum of Zoology, Ann Arbor, Michigan. Known office of publication: Department of Zoology, Mississippi State University, Mississippi State, Mississippi 37962.

Second class postage paid at Mississippi State, Mississippi and at additional mailing office.

PRINTED IN U.S.A. Allen Press, Inc., Lawrence, Kansas 66044

A Rufous Flycatcher, *Myiarchus semirufus,* perches near its nest in the dark recesses of a clump of *Acacia macracantha.*

Watercolor painting by Christopher M. Pineo, from a photograph taken near Chimbote, Peru, on 26 December 1973.

THE WILSON BULLETIN
A QUARTERLY MAGAZINE OF ORNITHOLOGY
Published by the Wilson Ornithological Society

VOL. 87, No. 4 DECEMBER 1975 PAGES 441–608

BEHAVIOR AND GENERIC STATUS OF THE RUFOUS FLYCATCHER OF PERU

WESLEY E. LANYON

Other than references to its restricted range in northwestern Peru and to its uncertain generic status, there is little in the literature on the Rufous Flycatcher, *Myiarchus semirufus*. There had been no vernacular name in general use prior to the designation by Meyer de Schauensee (1966) of "Seaboard Flycatcher." Maria Koepcke, who up until her tragic death in 1971 probably had more field experience with this little known species than any other professional ornithologist, felt that "Seaboard Flycatcher" was misleading in its erroneous implication of restriction to a strictly coastal habitat. She suggested "Rufous Flycatcher" (Koepcke 1970) in recognition of the unique plumage coloration (see frontispiece) and after consultation with Eugene Eisenmann. Meyer de Schauensee later accepted this change of vernacular in the first separately issued "Addenda and Corrigenda" for his 1966 book.

More significantly there are no accounts of the breeding biology of this species. In my revision of the crested flycatchers of the genus *Myiarchus* it was essential for me to acquire field experience with *M. semirufus* and, hopefully, to find the nest and eggs and record its vocal repertoire. I am reporting here the results of 2 trips that I made to northwestern Peru in 1973 (22 February through 4 March, and 18 December through 29 December), and will indicate the relevance of these findings to the generic status of the Rufous Flycatcher.

DISTRIBUTION AND HABITAT

The range of the Rufous Flycatcher is one of the most restricted of all of the *Myiarchus* flycatchers of South America. The localities at which it has been collected or observed are confined to a narrow zone along the coast of northwestern Peru, extending from Tumbes near the Ecuadorian border south to the vicinity of the Rio Pativilca, 200 km north of Lima (Fig. 1).

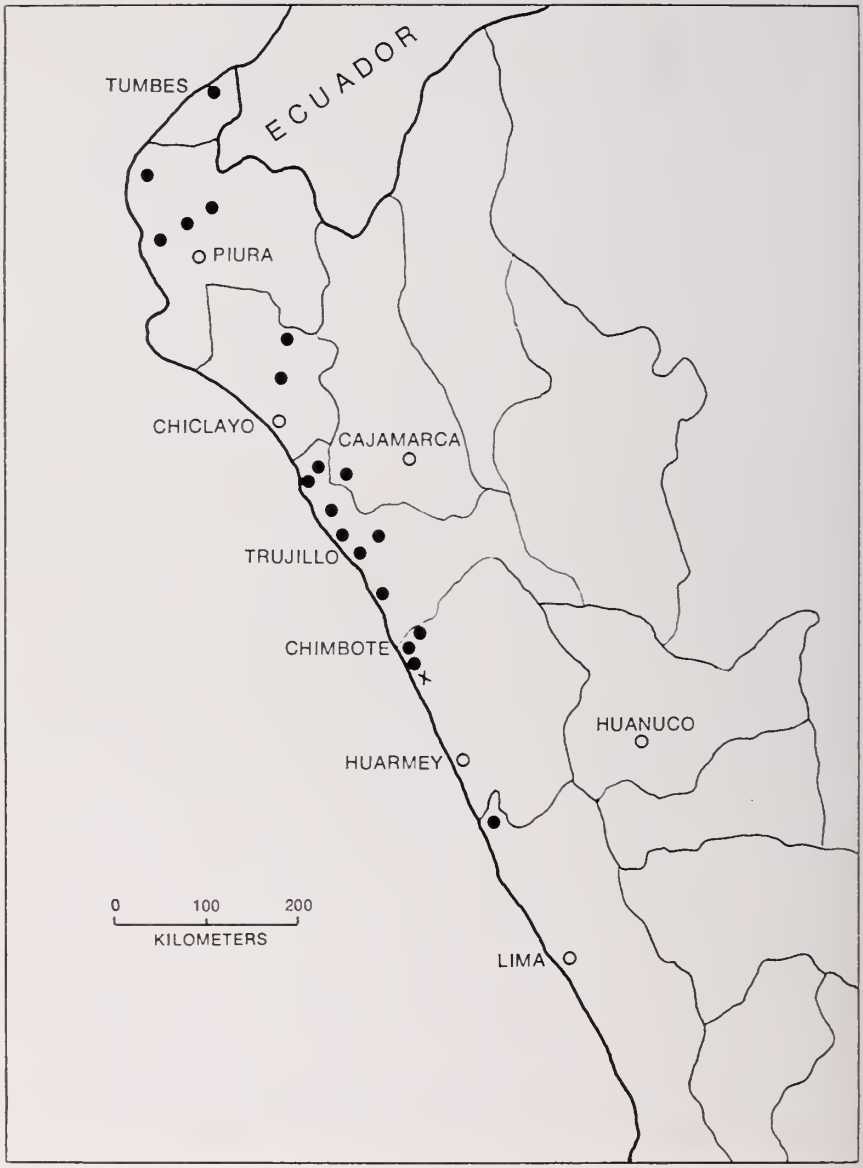

FIG. 1. Map of northwestern Peru, indicating localities (black dots) where the Rufous Flycatcher has been collected or observed. Localities and authorities are identified in the Appendix. The site of this study is marked with an x.

The width of this range generally is less than 50 km, being restricted on the east by the foothills of the Andes. I found a number of heretofore unreported localities for the species, but did not extend the distributional range either to the north or south, beyond that previously reported (Zimmer 1938, Bond 1947, Meyer de Schauensee 1966). Since the preferred habitat extends for some distance north into SW Ecuador, I feel that this flycatcher will eventually be found there as well.

The distribution of the species is entirely within, but does not occupy all of, those Peruvian life zones identified by Tosi (1960) as tropical, subtropical, or thorny desert. This extremely arid region owes its existence to the influence of the cold Humboldt current that flows north along the Peruvian coast. What precipitation there is generally comes as mist or fine drizzle associated with the fogs that blanket the region seasonally: during summer months (Jan.–Apr.) in the north, and during the winter (May–Sept.) in SE Peru. From Tosi's (1960, p. 261) table of climatological data for the coastal region of Peru, I estimate that the mean annual temperature is 24.2° C at the extreme northern end of the species' range, and 18.8° C at the extreme southern end of the range. The mean annual rainfall is given as 181 mm at the northern end of the range and only 24 mm at the southern end.

It is possible to drive for many kilometers through this desert habitat along the coastal highway of Peru (Pan American Highway) without seeing any vegetation or with only sporadic views of widely scattered clumps (Fig. 2). Only where permanent rivers, originating in the snowfields and glaciers of the high Andes, reach the sea does one encounter vegetation, land of potential agricultural use, or human settlements. Here the land is irrigated and used for growing sugar cane, rice, cotton, and other crops. Formerly there were extensive stands of small to medium trees (mesquite, *Prosopis* spp.; acacia, *Acacia* spp.; willows, *Salix* spp.; *Capparis* spp.) associated with these permanent rivers, but wooded areas are now confined to regions where topography or lack of irrigation discourages cultivation. Even in such areas, the larger trees are quickly cut for firewood and fence posts.

The localities where I was most successful in locating the Rufous Flycatcher were open thorn-woodlands dominated by mesquite and acacia trees. Often the trees were widely separated by sparse grasses and herbs. Koepcke (1970) characterized the species as "typical of the xerophytic steppes and mesquite savannahs."

Nowhere did I find this flycatcher common, and at no locality could I be certain of having observed or heard more than 2 adults. In fact, it was only after I obtained sufficient recordings to use a playback tape that I was able to locate birds with any degree of regularity or predictability. A low popula-

FIG. 2. The tropical desert habitat used by the Rufous Flycatcher. This is a portion of the study area marked with an x in Fig. 1. The utility poles border the Pan American Highway. A nest of this flycatcher was in the large clump of *Acacia macracantha*, center right.

tion density is characteristic of most *Myiarchus* flycatchers, however, for each pair apparently requires several hectares of suitable habitat in which to forage. Most wooded areas within the coastal desert of Peru are small and each such locality may be capable of supporting no more than a single pair of Rufous Flycatchers. This low density, coupled with the fact that it is not a very vocal flycatcher, accounts for the difficulty in locating the species: many bird watchers who have visited Peru's coastal region have failed to find it.

Some of the avian associates of the Rufous Flycatcher at the study area shown in Fig. 2 were the Croaking Ground-Dove (*Columbina cruziana*), Groove-billed Ani (*Crotophaga sulcirostris*), Lesser Nighthawk (*Chordeiles acutipennis*), Amazilia Hummingbird (*Amazilia amazilia*), Coastal Miner (*Geositta peruviana*), Baird's Flycatcher (*Myiodynastes bairdi*), Vermilion Flycatcher (*Pyrocephalus rubinus*), Tawny-crowned Pygmy-Tyrant (*Euscarthmus meloryphus*), White-crested Elaenia (*Elaenia albiceps*), Peruvian Plantcutter (*Phytotoma raimondii*), House Wren (*Troglodytes aedon*), Long-tailed Mockingbird (*Mimus longicaudatus*), Cinereous Conebill (*Con-*

irostrum cinereum), White-thighed Meadowlark (*Sturnella bellicosa*), Blue and Yellow Tanager (*Thraupis bonariensis*), Streaked Saltator (*Saltator albicollis*), and the Hooded Siskin (*Spinus magellanicus*).

With the exception of the extreme northern end of its range, the Rufous Flycatcher is not sympatric with other *Myiarchus*. It is not found far enough up the Andean slopes to overlap the distribution of *M. tuberculifer*. Locally within the northern departments of Piura and Tumbes, *M. semirufus* may occur in the same open thorny woodland as *M. phaeocephalus*.

BREEDING BIOLOGY

Since there are no references in the literature to the breeding biology of this species, my only clues to the timing of breeding had to come from data on the labels of museum specimens and the degree of plumage wear or evidence of molt in the specimens. The latter information suggested a difference of 1 to 2 months in the timing of the prebasic (annual, complete, post-breeding) molt between birds at the southern end of the range (departments of Ancash and La Libertad) and those at the northern end (Piura). Ancash specimens collected from February through April show various degrees of replacement of the flight feathers, while others taken as early as March and April are in fresh plumage. Piura specimens showing molt in the wings and tail have been taken in April and May and there are fresh plumaged June specimens. These data on molt suggest that the birds in the south breed from 1 to 2 months earlier than those in the north. It is probable that differences in the timing of the scant precipitation in this region and the resulting seasonality of the vegetation and insect populations are responsible for this asynchrony in the annual cycle of the Rufous Flycatcher.

In early March 1973, David Ewert and I found a group of 3 Rufous Flycatchers at a locality along the Pan American Highway about 50 km S of Chimbote, in the department of Ancash ("x" in Fig. 1) We observed them for a total of 6 hours over a 2 day period, during which time they were silent except for occasional renditions of a "huit" note (Fig. 6. 4–6). Two of these birds were adults, on the basis of their plumage, and one of these was completing its tail molt (median pair of rectrices half grown). The third bird, a juvenile, was collected. It had large "windows" in an incompletely ossified skull. On the basis of this information I believe this pair must have nested in December and January. Other avian associates at the same locality suggested a similar timing of breeding. Juveniles of the Long-tailed Mockingbird and Peruvian Plantcutter were present, and there were adult mockingbirds in obvious molt. None of the Vermilion Flycatchers were courting or displaying here, though we had found them doing so in Piura a few days

FIG. 3. The arrow indicates the location of a nest of the Rufous Flycatcher, located in a darkened recess of the clump of *Acacia macracantha* seen in its entirety in Fig. 2. A swath of vegetation and debris had to be removed to permit access and photography.

earlier. Further, there was very little song at dawn from any species at this locality. During our observations the Rufous Flycatchers spent most of their time foraging for insects at low to medium levels within the woody vegetation, in typical *Myiarchus* fashion. When stimulated, they would raise the feathers of the crown in a manner characteristic of the genus. One of them plucked and swallowed a small bluish berry. We searched the area for potential nest cavities but found none. Is the Rufous Flycatcher a cavity-nester like all other *Myiarchus*?

I returned to the study area near Chimbote in late December, accompanied by my wife and determined to find a nesting pair of these birds. It was encouraging to find that many of the avian associates were breeding, thus confirming my prediction. The Vermilion Flycatchers were going through their aerial displays, mockingbirds were feeding recently fledged young, and the chorus of song at dawn was vigorous enough to indicate rather widespread breeding.

Our initial efforts to discover breeding in the Rufous Flycatcher were in vain, though we located one pair quickly and found them to be more vocal than they had been in March. On 20 December I noted that they appeared to be courting, for there were occasional aerial pursuits and one instance of attempted copulation. But on 3 mornings I was unable to identify any components of the dawn chorus as the dawn song of this flycatcher, though by this time I had recorded a variety of daytime vocalizations and therefore had a fair idea of what to expect by way of dawn song, if in fact the species possessed one.

On 25 December my wife spotted one member of the pair carrying a white feather in its bill. I followed this bird for about 10 min as it moved through its territory, carrying the feather all the while, until it eventually entered a clump of *Acacia macracantha* (Fig. 2). A subsequent vigil and observations of the behavior of the pair of Rufous Flycatchers at this site led to the discovery of the nest on the next day. The nest, about one meter above ground level, was well hidden in a darkened recess of the acacia (Fig. 3). Though it was an open cup (Fig. 4) and not located within a tree cavity in the typical manner of *Myiarchus*, the light intensity at the nest was extremely low due to the impenetrable mass of dead branches and accumulated litter from the foliage of previous growing seasons. Much of this nest cover had to be removed to permit closer inspection and subsequent collection of the nest. Photography at the nest was made difficult by the contrast between the low light intensity normal to the site and the brighter light introduced by the removal of surrounding cover.

Though *Myiarchus* flycatchers normally use cavities within wood, they have been known to select other sites that provide equally low light intensities at the nest. In May 1959, near Tapachula, in Chiapas, Mexico, I observed a pair of *M. tuberculifer* carrying nesting material into a darkened recess within a mass of dead fronds on a date palm. Burton (1973) has reported *M. ferox panamensis* nesting in a burrow in a roadside bank. There are no woodpeckers in the southern two-thirds of the range of the Rufous Flycatcher and natural tree cavities large enough for use by this flycatcher are scarce. All dead or dying timber is quickly removed for firewood and

FIG. 4. Close-up of the nest. One of 3 eggs is visible, as well as the typical *Myiarchus* lining of fur and feathers.

living trees seldom are permitted to reach a girth that might be suitable for a hole-nesting species of this size. We found no other nests of the Rufous Flycatcher, and can only speculate that, at least throughout the southern part of its range, this species commonly may resort to selecting the darkened recesses within clumps of acacia in the absence of tree cavities.

With respect to the materials used in its construction, the nest was typical of that of other members of the genus. It was lined with fine and coarse fur, numerous pieces of shed reptilian skin, fragments of tissue paper, newspaper, and clear plastic, and a few white feathers (Fig. 4). The fragments of shed reptilian skin were from at least 2 species of snakes and one species of lizard.

The 3 eggs in the nest had been incubated for about 2 days when collected on 26 December. In size, shape, ground color, and markings they are well within the range of variation one finds among the eggs of *Myiarchus* flycatchers (Fig. 5). The ground color is a creamy white, and the irregular markings and blotches of brown and brownish lavender are more concentrated at the larger end.

The female of the pair at this nest was collected on 26 December. She weighed 25.0 g and had a well-developed brood patch; her oviduct and ovary were much enlarged. The male was not collected until 3 days later, in order

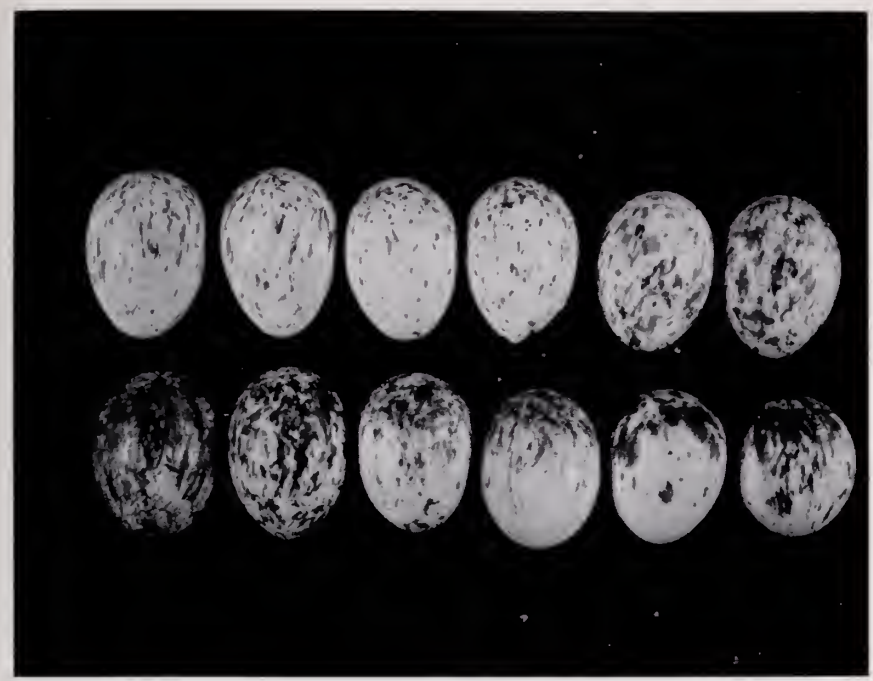

FIG. 5. Comparison of the eggs of the Rufous Flycatcher (median pair, top row) with those of 3 other species of *Myiarchus*. The 3 pairs of eggs in the top row, left to right: *M. tyrannulus*, Colombia; *M. semirufus*, Peru; and *M. cinerascens*, California. The 3 pairs of eggs in the bottom row illustrate the considerable intraspecific variation in the eggs of *M. crinitus*: left to right, a pair from South Carolina, and 2 pairs from Florida.

that I might obtain more tape recordings, particularly of its dawn song. He weighed 23.0 g and his testes were 10 mm by 6 mm. Both birds had fully ossified skulls, completely black bills, and yellow mouth linings.

Two other adults in breeding condition were collected south of Chimbote, in Ancash department in late December. A male, taken on 28 December, weighed 24.0 g and had testes that were 10 mm by 5 mm. A female, taken on 29 December, weighed 22.0 g and had the initial stages of a brood patch. Another adult female, collected on 21 December just north of Paijan, in La Libertad department, about 220 km north, weighed 21.0 g and was not yet in breeding condition (ova less than 1 mm diameter; no developing brood patch). This corroborates my earlier conclusion based on molt data that Rufous Flycatchers in the southern part of their range breed earlier than those in the north.

VOCALIZATIONS

The basic vocal repertoire of the Rufous Flycatcher, as determined by the recordings that I made of 2 breeding pairs and of several non-breeding individuals, consists of 5 different notes. This repertoire size is consistent with what I have found in other *Myiarchus*. Likewise, the individual notes have counterparts in the vocalizations of other *Myiarchus*.

The note most heard from these flycatchers while they are foraging, particularly from non-breeding individuals and birds not stimulated by territorial intruders or by playback of sound recordings is the "huit" note (Fig. 6, 4–6). It may be given by either sex, is at a low intensity and hence does not carry far, and is rendered singly. To my ear it is indistinguishable from a note of the Vermilion Flycatcher, given under similar circumstances.

When the incubating female left the nest, she was joined by the male and the pair foraged together, often covering several hectares of the male's territory. Particularly during the first few minutes following the reunion of the members of the pair and presumably in response to such stimulation, simple unmodulated and descending whistles might be rendered, either singly or in short series (Fig. 6, 10–11). I can not be certain that I heard both sexes give these whistles, though I believe they did. All evidence suggests that the sexes of *Myiarchus* have identical vocal repertoires. The only reference in the literature to the voice of the Rufous Flycatcher is Taczanowski's (1884) quotation from the field notes of Jelski: "Its voice is a monotonous whistle, repeated from time to time." The reference may have been to this whistle, or it may have been to the rasping, piercing type of whistle described next.

In circumstances of more intense stimulation, as when confronted with the presence of an intruder or with the sounds of a playback tape, either sex of a breeding pair may give a sharp rasping whistle, either singly or in rapid series. This whistle is modulated at a moderate rate of 50 to 60 cycles per sec. which lends a definite rasping quality to the note (Fig. 6, 7–9). In moments of intense excitement, the pair may vocalize in a duet, using this rasping whistle almost exclusively but occasionally interjecting a "hic-up" note or "brrrt" note.

Another note given by members of a breeding pair during periods of intense excitement is one I have labelled the "hic-up" note (Fig. 6, 15–16). It appears to be derived from modifications of the "huit" note, and sometimes includes the "brrrt" note (see below) as one of its components. It is usually heard by the human ear as a 2 or 3 syllabled note.

The "brrrt" note (Fig. 6, 12–14) sometimes is rendered singly as a conversational note between members of a foraging pair and sometimes is included as a component of the "hic-up" note. The modulation of the carrier

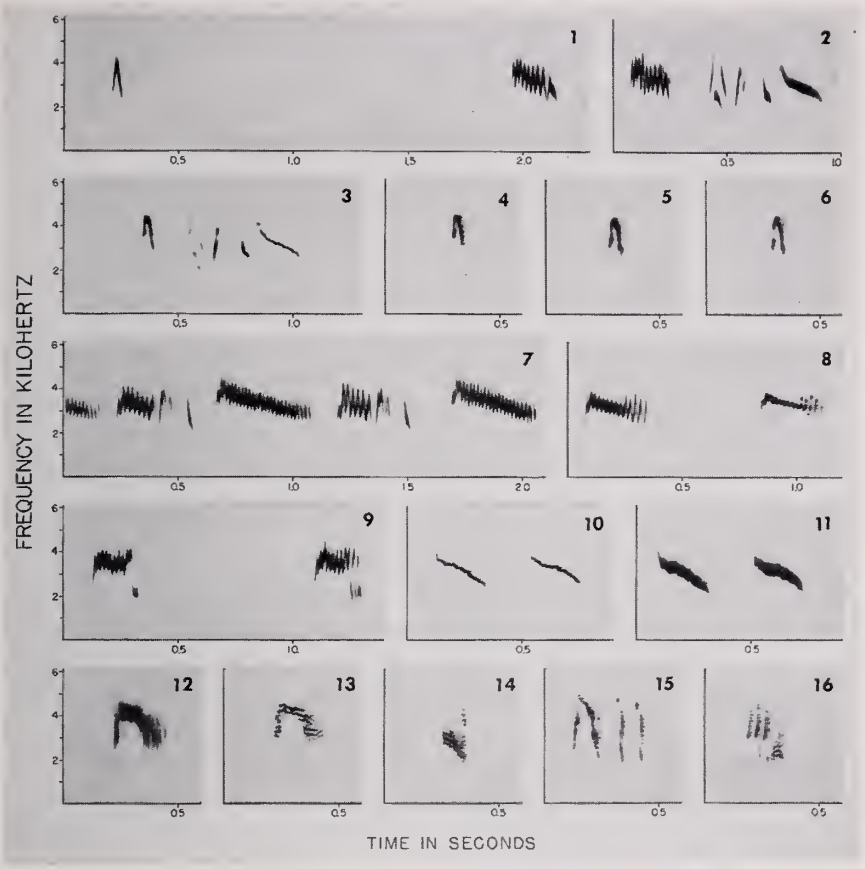

Fig. 6. Sound spectrograms of vocalizations of the Rufous Flycatcher: 1–3, components of the dawn song; 4–6, variations of the "huit" note; 7–9, variations of the rasping whistle; 10–11, descending whistles; 12–14, variations of the "brrrt" note; 15–16, variations of the "hic-up" note. Recorded 50 km S of Chimbote, Peru, between 25 and 29 December 1973, with a Uher 4000L tape recorder, preamplifier, and a Uher microphone mounted in a 61 cm parabolic reflector. Graphs were made on a Sona-Graph, model 6061B; the narrow band filter was used for displays 3, 4–6, 10, 13–16; the wide band filter was used for displays 1, 2, 7–9, 11, 12.

frequency of this note is about 3 times as rapid as in the case of the sharp, rasping whistle. This note has a counterpart in the repertoire of most *Myiarchus*.

The males of each *Myiarchus* species give a stereotyped, species-specific pattern of vocalizations just prior to and at dawn, beginning at the onset of territorial defense and extending for varying lengths of time through the

remainder of the breeding season. Many but not all genera of tyrannid flycatchers exhibit this vocal behavior, which has become known in the literature as the "dawn song." Each component of the dawn song can be heard as individually-rendered notes during the day: i.e., there are no components unique to dawn song. The arrangements of these components into predictable patterns having consistent temporal characteristics, and the repetition of these patterns in a nearly unbroken sequence for a period of 15 to 30 min at dawn each morning during the breeding season are unique features of this dawn song.

In my brief exposure to the breeding pair of Rufous Flycatchers at the study area in Ancash, I heard the male give dawn song on the morning that the female and nest were collected (second day of incubation) and again 3 mornings later, at which time the male had attracted a new female that showed the beginnings of a brood patch. I believe I could have recorded him for at least 2 weeks prior to the onset of incubation, had I been there and had I been able to recognize the vocalization as that of the Rufous Flycatcher.

The dawn song of this flycatcher consists of isolated and alternated renditions of "huit" notes and rasping whistles (Fig. 6, 1), with frequent interjection of a more complex component derived from a combination of a modified "hic-up" note and a simple descending whistle. This complex component is given less frequently than the other notes, and always follows in rapid sequence the rendition of either a "huit" note or a rasping whistle (Fig. 6, 2–3). A normal dawn song sequence might include the alternated renditions of "huits" and rasping whistles for 10 or 15 sec, and then a complex component introduced by a rasping whistle. After another sequence of alternated "huits" and rasping whistles, a complex component introduced by a "huit" note might follow.

GENERIC STATUS

In their original description of *Myiarchus semirufus*, Sclater and Salvin (1878) concluded that "although so abnormal in colour, we cannot arrange this bird . . . as otherwise than a typical *Myiarchus*." However, following a contrary opinion expressed earlier by Berlepsch (1907), Bangs and Penard (1921) assigned *semirufus* to a new, monotypic genus, *Muscifur*, and cited as their reasons a difference in the shape of the bill and the wing and the unique color of the plumage. In his revision of South American *Myiarchus*, Todd (1922) commented on Bangs and Penard's new genus: "Every one of the diagnostic structural characters claimed for it by these authors we find repeated in typical *Myiarchus*, leaving only the different color-pattern to be considered, and an additional character in what appears to be the rougher scutellation of the tarsi. Whether under the circumstances *Muscifur*

deserves recognition is an open question. Probably it would be better to keep its type in *Myiarchus* in spite of its aberrant coloration." Hellmayr (1927) agreed with Todd in discounting the importance at the generic level of the peculiar color pattern and the slightly rougher scutellation of the tarsus. He placed *semirufus* at the end of his catalogue entries for *Myiarchus*, next to 2 other flycatchers that he preferred to assign to separate monotypic genera (*Hylonax* and *Eribates*) but that have subsequently been placed in *Myiarchus* by Zimmer (unpublished MS) and subsequent authors.

It was Zimmer's (1938) analysis of *semirufus* that most influenced later workers: "This bird stands somewhat apart from the general assemblage of species in the genus *Myiarchus* in which it appears to have no very close relative. The color is predominantly rufous instead of gray and yellow: the plumage is rather coarse in texture: the crest is rather long; the scutellation of the tarsus is a little rougher than usual: the bill is relatively long, somewhat flattened, and convex in lateral outline to near the narrow tip. Nevertheless, except for the color, the characters are not perfectly diagnostic. The tiny tubercle on the underside of the wing at the base of the outer primary is present as in other members of *Myiarchus* (as well as in *Hylonax* and *Eribates*), pointing to close affinity. I believe that *Muscifur* of Bangs and Penard, erected for *semirufus*, is of good subgeneric value but that it is not entitled to full generic rank." Subsequent authors have followed Zimmer in retaining *semirufus* in *Myiarchus* (Bond 1947: Meyer de Schauensee 1966, 1970; Koepcke 1970), without exception to my knowledge, but place it either at the beginning or at the end of the species accounts in recognition of the degree of divergence from and the uncertain affinities with its congeners.

My observations on behavior and breeding biology support Zimmer's conclusion based on morphology, i.e., that *semirufus* is best retained within *Myiarchus*. Agreement between the Rufous Flycatcher and other *Myiarchus* has been established on the following points: foraging behavior: tendency to erect the feathers of the crown when stimulated: preference for extremely low light intensity at the nest site: prolific use of fur, feathers, shed reptilian skin, and paper or plastics in the nest lining; size, shape, ground color, and markings of the eggs; and vocalizations, in terms of repertoire size, actual components, and rendition of a dawn song.

SUMMARY

The little known Rufous Flycatcher is restricted to the coastal desert of northwestern Peru. Its predominantly rufous color sets it apart from other *Myiarchus* and has contributed to its uncertain generic status. Data presented here on the species' behavior, nest, eggs, and vocalizations support Zimmer's conclusion, based on morphology, that the Rufous Flycatcher is best retained in *Myiarchus*.

ACKNOWLEDGMENTS

This study was supported by the Leonard C. Sanford Trust Fund of the American Museum of Natural History. I am grateful to David Ewert, Vernia H. Lanyon, and Thomas Jacikoff for assisting with the field work, and to Manuel Plenge of Lima, Peru, and Hernando Macedo, Museo de Historia Natural "Javier Prado," in Lima, for courtesies and assistance. Ned K. Johnson gave me a sight record locality and Eugene Eisenmann provided the background for the derivation of the vernacular name. Larry Pardue of the New York Botanical Garden confirmed my identification of the acacia in which the nest was found, and Charles Myers of the American Museum of Natural History's Department of Herpetology gave me a determination on the fragments of shed reptilian skin.

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Appendix

List of Peruvian localities, by department, where *Myiarchus semirufus* has been collected. In addition, the localities for 3 sight records have been included, as indicated. The authorities for these localities are given in parentheses.

Tumbes: Tumbes (Sztolcman).

Piura: 15 km E of Talara, sight record (Ned K. Johnson); Somate (Watkins); Chilaco (Watkins); Pilares (Watkins); 23 km NE of Paita, sight record (Lanyon); Sullana (Bangs and Noble).

Lambayeque: Olmos (Carriker); 55 km NE of Chiclayo, sight record (Lanyon).
Cajamarca: Tembladera (Baron).
La Libertad: Chepen (Sztolcman, Baron); Guadalupe (Carriker, Raimondi); Pacasmayo (Steere, Sztolcman); Cartavia (Carriker); 5 km N of Paijan (Lanyon); Trujillo (Baron); Virú (Watkins).
Ancash: Hacienda de Suchiman (Carriker); Chimote (Sztolcman); 33 km N of Casma (Lanyon); 10 km N of Casma (Lanyon).
Lima: Huariconga (Birdseye); Paramonga (Carriker).

AMERICAN MUSEUM OF NATURAL HISTORY, NEW YORK, NY 10024. ACCEPTED 23 DEC. 1974.

NEW LIFE MEMBER

Dr. William H. Elder, Rucker Professor of Forestry, Fisheries & Wildlife at the University of Missouri, Columbia, Missouri is now a life member of the Wilson Ornithological Society. Dr. Elder is primarily interested in waterfowl biology and management and in the population dynamics of permanent resident passerines. He has published extensively in the professional and popular literature. Dr. Elder is married and has two children. In addition to his ornithological activities he is interested in wildlife photography and canoeing.

SUGGESTIONS FOR CALCULATING NEST SUCCESS

Harold F. Mayfield

Reports of nesting success that do not take into account the time span of observation for each nest usually understate losses, and sometimes the error can be very large. More than a decade ago I pointed out this problem and proposed a way of dealing with it (Mayfield 1960:192–204; 1961). Since that time many field students have used the method, and it has proved especially helpful in combining fragments of data from many sources, as in the North American Nest-record Program at Cornell University. However, not every published report shows awareness of the problem, and letters of inquiry have shown that some people are deterred from dealing with it because of difficulty with details. Therefore, I offer these further suggestions to simplify the procedure as much as possible.

THE PROBLEM

All nests are not found at the very start. Indeed, most nests of small open-nesting birds are not found until incubation is well under way or until the young have hatched. The observed success in such a sample will be greater than the true nesting success of the species.

The shorter the time span of observations, the less the observed losses: that is, nest mortality—loss by destruction or desertion—is a function of time. Since nearly all field studies contain a mixture of nests found early and late, as customarily reported they show nesting success higher than reality: but the amount of error is indeterminable because the time each nest entered the sample is not reported. For precise analysis of mortality and survival, it is not enough merely to count nests, eggs, and young. The elapsed time of the observations must also be considered.

To illustrate the main difficulty, suppose you found a series of nests when incubation was far advanced. Hatching success would be nearly 100%; and in nests containing large young when found, fledging success would be nearly 100%. Yet you would hesitate to present these figures because it is plain that not enough time elapsed for many accidents to befall. In this extreme case the pitfall is obvious, but in a mixed bag of data, this kind of error may slip through unnoticed.

What you are trying to determine is the nesting success of a population. Ideally you would like to find all the nests started by the birds in that population, watch all these nests from their beginnings, and observe everything that happened up to the fledging of young. Usually this is impossible and you have to settle for a good deal less, namely, a sample that is anything but

neat and complete. Some nests in the population are not found at all, some are not under observation for their full duration—found early, found late, or not followed to a conclusion.

What do you do with these incomplete records, which often comprise the larger part of the data? Customarily, some aspects of the problem are ignored. Nests found late are lumped with nests found early and considered alike. The result is to understate mortality and overstate success, as mentioned earlier.

Not everyone dodges the issue. In his study of the Yellowhammer (*Emberiza citrinella*), Peakall (1960) used only the subsample of nests observed from the very start. But this course brings 3 objections: First, very few field studies contain enough nests found before incubation began: second, the nests disqualified contain valuable information that should be used if possible: and third, the subsample of nests found earliest may not be typical. Perhaps they were easier to find because of their locations or because the vegetation concealing them was not yet far advanced.

In some elusive species the eggs and young may be found almost at random times throughout the duration of the nesting cycle. If so, the average period of observation is about half the duration of the nesting cycle, and the observed losses are about half the true losses. Coulson (1956) recognized this fact in his study of the Meadow Pipit (*Anthus pratensis*) and corrected the observed figures by doubling the known losses.

Up to this point I have discussed nests not observed from the start, but what of nests not followed to a conclusion? At one extreme there is the case of an ornithologist whose field records each year did not begin until he arrived at his summer cottage after the close of the school term, and at the other extreme are the members of expeditions and the vacationers who are obliged to leave a region while some nests are still active. Samples containing the work of many years are likely to contain records of both kinds.

Customarily, I suspect, nests with outcomes unknown are excluded from samples used in calculating success. Yet, this too is regrettable, because it tends to exaggerate losses. That is, a nest lost early becomes a part of the record, whereas a nest that persists is thrown out.

Finally, the sorriest data are those on nests whose beginnings are shrouded in doubt and whose outcomes are also unknown. These are certain to be discarded in calculations of success. The effect on the sample is uncertain, but any loss of data is regrettable and any discards may introduce bias.

No field student is happy to see a simple concept like nesting success made to appear complicated. Yet everyone who has undertaken a nesting study knows that his own data embody not only hard facts but also elements of judgment that might have been handled differently by another worker. None

of this difficulty is apparent in published tables of figures, which convey an air of indisputable finality.

A review of nest success in altricial birds by Nice (1957) is widely quoted. Yet Woolfenden and Rohwer (1969) examined about half the 35 summarized studies of open-nesting birds included: in not one did the original author tell how he dealt with these difficulties. Ricklefs (1969) offered a sophisticated analysis of mortality in small altricial birds but threw up his hands at trying to disentangle these tissues in published studies, and treated all nests as if "found before the initiation of laying."

It is true that nests of some species are more likely to be found during the building stage than during incubation, and some field workers—notably, the oologists—are particularly adept at finding nests before the eggs are laid, but these circumstances are not universal. My own experience in the field and consultations with others about their data lead me to suspect that raw data on species with hard-to-find nests commonly reveal a mortality only a little more than half the true mortality. This problem needs to be dealt with in one way or another.

In this whole discussion I emphasize small open-nesting birds, because the problem of finding nests early is much more acute in such species than in those nesting in boxes or other predetermined sites.

A SOLUTION

There is a straightforward way of dealing with these problems that makes use of nearly every bit of data collected. In principle it treats nests in terms of mortality and survival over observed periods of time. Survival is the converse of mortality. For mathematical elegance, we deal with both as probabilities.

Nest success may be viewed in 5 stages: (1) survival during the building of the nest; (2) survival during the egg-laying period; (3) survival during incubation; (4) hatching of eggs, which is assumed to take place at a point in time when the first young bird breaks free of the shell; (5) survival of young to fledging. Here I will focus attention on the last 3 stages.

The number of observed losses will depend on the number of nests in the sample and the amount of time each nest is under observation—that is, the *exposure*. A convenient unit for measuring exposure is the nest-day (one nest for one day). For example, 2 nests both under observation for periods spanning 6 days represent an observed exposure of 12 nest-days: this is equivalent to 3 nests observed for 4 days or one nest for 12 days. The time span is the crucial factor even though the nest was not actually visited on all the days in it. By dividing the total number of losses by the total number of nest-days, you get the mortality and survival rates (probability) for any period.

For the greatest precision by this method, if your sample were large enough, you might calculate a separate survival rate for each day of each stage, and compute the probability of survival for n days by the product $P_1P_2P_3 \ldots P_n$, where P_1 is the probability of survival on day 1, P_2 is the probability of survival on day 2, and P_n is the probability of survival on day n. However, very few studies will have samples of sufficient size to yield a reliable separate rate for each day. So, if losses do not bunch up early or late in any stage, the practical course is to calculate an average mortality and survival rate across each stage of the nest. Since the conditions at the nest are usually different for each stage, we would expect to find, for example, a survival rate during incubation different from the survival rate during the nestling stage.

Here is an example. In my study of the Kirtland's Warbler (*Dendroica kirtlandii*) (Mayfield 1960:193), 35 nests were lost during 878 nest-days of incubation, and the mortality was therefore $35/878 = .040$ per nest-day. If so, the survival rate was $1 - .040 = .960$ per nest-day. Now we can use what we have learned from the entire sample to predict the probability of success for a nest through the full 14 days of incubation. Since the probability of successive events is the product of their probabilities, the probability a nest will survive 14 days is .960 multiplied by itself 14 times, or $.960^{14} = .56$.

In raising decimals to high powers, it is best to use as many decimal points as practical at each step, because repeated rounding off of decimals will cause errors to pyramid.

In calculating nest success—defined as the survival of any contents of the nest—you ignore partial losses through the failure of some but not all eggs to survive and hatch, and proceed immediately to the nestling period, which you handle in the same way. For example, in the Kirtland's Warbler (Mayfield 1960:198) in 735 nest-days with young in the nest, 22 nests were lost. So the mortality rate was $22/735 = .030$ per nest-day, and the probability of survival was $1 - .030 = .970$ per nest-day. Hence, with a nestling period of 9 days, the probability of survival of a nest with young was $.970^9 = .76$.

Combining these probabilities, we have the probability of survival of a nest from the start of incubation to the fledging of young, $.56 \times .76 = .43$. Note that nest success is usually somewhat larger than egg success, because some eggs do not hatch and some eggs and young are lost from nests whose contents otherwise remain intact.

A separate calculation gives the hatching rate—the probability that eggs present at hatching time actually produce living young. Divide the number of young by the number of eggs present just before hatching. In Kirtland's Warblers (Mayfield 1960:197) this probability was .73: that is, 27% of the eggs present at hatching time did not hatch.

If there are no significant losses of eggs or young without the loss of entire nests, the 3 probabilities calculated in the previous paragraphs may be combined to arrive at the probability an egg present at the start of incubation will produce a fledgling. We multiply the probability an egg will survive the incubation period, by the probability an egg will hatch, by the probability a young bird will survive the nestling period: thus, $.56 \times .73 \times .76 = .31$.

In some species a considerable number of eggs or young may vanish from nests that are not lost totally. If so, the probability of these events must be superimposed on the previous calculations. The principle is the same, but now it is necessary to introduce a smaller unit of exposure, the egg-day or the nestling-day. That is, a nest with 5 eggs observed for one day has an exposure of 5 egg-days. Similarly, nestling-days measure the exposure of young in the nest. Note that when more than one egg or nestling is in the nest, the exposure in egg-days or nestling-days is much larger than when measured in nest-days, and for nests not suffering internal variations, it is a multiple of the number of nest-days.

The total number of individual eggs lost without the loss of all eggs in the clutch divided by the total number of egg-days gives the mortality per egg-day. For example, in the Kirtland's Warbler I noted 6 eggs lost individually during incubation where the exposure was 3131 egg-days. (This number was small because most eggs removed by cowbirds vanished before incubation began.) The mortality was .002 and the survival was .998 per egg-day, and the probability of an egg surviving the incubation period in a persisting nest was $.998^{14} = .97$. A similar calculation may be made for nestlings surviving in persisting nests.

Often, as in my example, these categories of loss are very small, or, conversely, the probability of survival of eggs and young in continuing nests is very high. If so, it is doubtful if this refinement is justified by the limited accuracy of the basic data. However, to pursue the example given, if the only adjustment to be made is for eggs lost individually, we multiply this last probability by the previously calculated probability of survival of nests from the start of incubation to fledging (which ignored losses of individual eggs and nestlings) and get a slightly reduced probability of success: $.97 \times .31 = .30$. If there is also a significant loss of individual nestlings, this will call for a further adjustment downward of the ultimate probability of success from the start of incubation to fledging.

ARE MORTALITY RATES OF SEPARATE STAGES REALLY DIFFERENT?

In the foregoing example I have treated the incubation period separately from the nestling period (ignoring nest-building and egg-laying stages). This step may not always be necessary. In precocial birds the nestling period

Table 1

Comparison of Mortality in Incubation and Nestling Periods of Kirtland's Warbler*

	Nest-days with losses	Nest-days without losses	Total nest-days
Incubation period	35	843	878
Nestling period	22	713	735
Totals	57	1556	1613
$\chi^2 = 1.16$, $P > .25$			

* This contingency table, constructed to appraise by the chi-square test if there is a real difference in mortality between the incubation period and the nestling period, shows that the observed difference might have been expected by chance in about a quarter of samples of this size; i.e., a significant difference is not proven, although a larger sample might show a real difference to exist.

shrinks toward the vanishing point, and in some altricial birds the mortality in the two periods may not be significantly different.

To appraise the difference, we construct a 2×2 contingency table, as shown in Table 1, and apply the chi-square test. The test reveals the observed difference is not statistically significant for the entire population at a high level of probability. This is plausible because the variants (losses) are relatively small numbers, and chance effects could have a major influence on the differences. Therefore, on the basis of this sample, the observed difference cannot be taken as virtually certain; that is, the difference does not meet the 1% or 5% test of significance commonly used by statisticians to be assured the difference could be explained on the basis of chance alone in less than 1 or 5 times out of 100. However, the difference may still be real. A larger sample might increase the confidence level.

Changing to a smaller unit—say, nest-hours—might seem to hold out promise of a different result, since it multiplies the sample size without enlarging the losses; but in this instance it still yields a chi-square and probability of the same order, and therefore does not alter the general conclusion.

In these circumstances, what are the alternatives? By lumping the 2 stages, you enlarge the sample and increase the confidence in the single mortality rate across both. Sometimes this is the wise course. Yet, to do so, may mask real differences that ought to be recognized for some purposes. It would be astonishing to find survival rates identical in the 2 stages, since desertion is usually more prevalent during incubation and predation is usually more likely when activity at the nest increases after the hatching of young. The observer should state reasons for whatever course taken.

In this example, lumping the stages to get a single rate brings little change

in the final results. The survival rate per day for the entire 23 days of incubation and young is .96466 (instead of .96 and .97 for the respective stages). Using this rate for both, we find the probability of survival for the incubation period is .60 (instead of .56): for the nestling period is .76 (the same as before); for the product of the two is .46 (instead of .43): and for the entire 23 days of both stages considered as a unit is .44. At no point do the 2 methods give survival probabilities differing by more than .04.

SOME CAUTIONS

A basic underlying assumption of this method is that mortality is approximately even across each stage. That is, we judge in a particular study that nests are about as likely to fail early in incubation as late in incubation, and about as likely to fail early in the nestling period as late in the nestling period. For several species I have examined, this appears to be true, but to prove it rigorously would require a very large sample. Lacking this, we may judge the distribution of losses approximately by inspecting the total losses for each day in the nesting cycle, which may be entered at the foot of the column for each day on the worksheet suggested here. A notable concentration of losses anywhere should be apparent.

In the Mourning Dove (*Zenaida macroura*), which builds a flimsy and often exposed nest, Woolfenden and Rohwer (1969:38) found losses within the incubation period much more likely to occur near the beginning. So a flat mortality rate across the incubation period proved inappropriate for analysis of this portion of the nesting cycle.

The unit of time suggested here is one day, because nests are commonly visited on a daily schedule and recorded by days. Many observers avoid visiting a nest more often than once a day lest they interfere with its normal progress. Skutch (1966:5) expressed concern about visits even this frequent and saw here an objection to the use of this method.

Intuitively one feels some predators may follow human beings to bird nests, but it is also possible some predators may be repelled by the presence or scent of people—as fur trappers tend to believe. In any case, we are faced with a kind of biological "uncertainty principle" whereby any nest observed is no longer in its *natural* state.

Willis found a way to compare survival rates of visited and unvisited nests of Bicolored Antbirds (*Gymnopithys bicolor*) in the forest of Barro Colorado Island, Panama. Applying his test, he found "survival rates of visited and unvisited nests are very similar" (Willis 1973:264).

However, daily visits are not a cornerstone of this method. Rather, the key concept is the *time span* of observations, which may be measured even though days may be missing from the record. The emphasis here is not on the way information is gathered but on the way it is used after it is collected.

Table 2

Sample Entries in Worksheet, Left Side

Nest no.	Incubation: Egg-days	Incubation: Nest-days	Days before hatching: −17	−16	−15	−14	*−13	−12	−11	−10	−9	−8	−7	−6	−5	−4	−3	−2	−1	0**	Comment
73–1	69	14	1	2	3	4	5	5	5	5						5	5	5	5	4/1	1. Gap in record.
73–2	50	10								5	5	5	5	5	5	5	5	5	5	3/2	2. Start not observed.
73–3	24	5				4	5	5	5				0								3. Nest destroyed.
74–1	14	3			3	4	5	5	5												4. Nest deserted.
74–4	19	4				4	5	5	5	5											5. Human disturbance.
Totals																					
Losses by days																					
												Unknown chronology									
74–2	25	5					5	5	5	5	5	5									6. Start & outcome unknown.
74–3	0	0					5														7. One visit only.

* Incubation begins on next-to-last egg, day −14.
** Hatching begins on day zero.

Table 3

Sample Entries in Worksheet, Right Side

Nest no.	Days after hatching												Nests with young		Comment
	0	+1	+2	+3	+4	+5	+6	+7	+8	+9	+10	+11	+12	Nest-days	Nestling-days	
73–1	4	1	5	5	5	5	5	5	5	5	5			10	50	8. Record complete.
73–2	3	2	5	4	3	3	3	3	3	3	3			10	33	9. Partial loss.
74–5						4	4	4	4	0				3½	14	10. Age estimated.
																11. Total losses by days.

There is nothing magic about a day as a unit. Conceivably, with automatic recording of events in the nest, a half-day or an hour might suit special purposes. However, we should be wary of being lured into a fictitious appearance of precision. Any method we use will give no more than an approximation of the truth, and this method merely helps avoid certain gross errors that are common. In birds with very long nesting periods and widely spaced visits, time units larger than one day may be suitable. By using the largest practical unit, we minimize the pyramiding of small errors when raising inexact numbers to high powers.

In addition to matters treated here, there are many problems that are not circumvented by mathematics. In samples of modest size, stochastic variables may be important and seriously interfere with generalization to larger populations. Fortuitous influences may vary from year to year and place to place —predation, competition, weather, sex ratios, and so on.

WORKSHEET

You will simplify analysis if you enter all your nest data on one large worksheet. I prefer to use ruled ledger paper, splicing sheets together to any desired width and length. For hundreds of nests the sheet may be so long it must be rolled like a scroll or folded like a computer printout.

Table 2 illustrates the left portion of such a sheet (egg-laying and incubation), and Table 3 illustrates the right portion of the same sheet. A "Comment" column is useful for noting special circumstances when entering data on the sheet, but I have used it here to identify some common problems selected for illustration. In this example I focus on the nest stages from the start of incubation to the fledging of young. Similar attention may be given to nest-building and egg-laying stages if the samples are large enough.

1. *Gap in record.* Nest 73–1 (code designates nest No. 1 of 1973) was not visited for a period of 5 days, but this did not detract from the record in any way, since no change in nest contents occurred in the interval. On handwritten worksheets it is convenient to circle all numbers representing eggs.

2. *Start not observed.* Nest 73–2 was found during incubation, and these entries were positioned on the table after the hatching day was determined.

3. *Nest destroyed.* Nest 73–3 was not visited between day –11 and day –7, when it was empty. Destruction is assumed to have occurred midway between the last two visits, namely, on day –9. If the gap in observations had been between day –11 and day –8, the midpoint would have been day –9½, and this would be taken into account in the nest-day and egg-day entries at left, where fractions present no difficulties. The estimated failure date is not precisely at the midpoint between the 2 observations; it is a little earlier, but not enough to make an appreciable difference for these purposes. (If the loss rate is constant, the numerical size of the losses declines steadily, and therefore the mean age of those lost in any time interval will always be less than the mean point in the interval.)

4. *Nest deserted.* Nest 74–1 was not attended by adults and the eggs were cold when it was visited on day –11. Desertion is assumed to have occurred on the day when noted since the nest was active the previous day. An extra visit or some other clue often gives the observer an inkling about the time at which the loss occurred that is better than any arbitrary rule. The observer's judgment might place this loss at day –11½.

5. *Human disturbance.* Nest 74–4 was subjected to experimental removal of eggs on day –9, and the nest was promptly deserted as a result. This record was admitted to the sample for 4 days of its observed period but disqualified henceforth. A portion or all of a record may be excluded for any human disturbance judged serious enough to affect the outcome, such as a gross alteration in the environment, photography, or other disruptions.

6. *Start and outcome unknown.* Because of their unknown chronology, nests 74–2 and 74–3 are segregated so they do not figure in any totals by days. Nest 74–2 was visited on 6 successive days, which constitute a time span of 5 days observation. Although this record cannot be used in analysis of events attributed to specific days, it can be used as a part of total exposure during incubation. With some species the extent of incubation may be judged by examination of the eggs, but this is not always feasible.

7. *Single visit.* Nest 74–3 was visited only once and therefore is excluded from all calculations because the period of observation does not cover a full day. Entries must show observations on 2 days, separated by at least 24 hours, to constitute a time span of a day or more. A nest visited only once may provide data for other purposes, but it is not useful for records of mortality and survival. The exposure in nest-days is zero.

The remaining examples appear on Table 3, representing the righthand side of the worksheet.

8. *Record complete.* Nest 73–1, appearing also in Table 2, remained intact until found empty on day +11. Fledging may be assumed even though the young are not seen, since young in this species sometimes leaves the nest as early as day +9. Finding all the fledglings after they have been out of the nest a few hours is very difficult in some species and unnecessary for this purpose, where attention is on survival for a stated period.

9. *Partial loss.* Nest 73–2 lost one young bird on day +2 and another on day +3, but the nest endured, and the remainder of the young fledged normally. The number of nest-days was not affected by the losses, but the number of nestling-days reflected them. Losses of individual eggs from continuing nests would be treated similarly in Table 2, the lefthand portion of the worksheet.

10. *Age estimated.* Nest 74-5 was found after hatching and destroyed before fledging, but an experienced observer can position the nest approximately in the table at his first inspection of the young.

11. *Total losses by days.* At the bottom of each column representing a day in the nesting cycle, you enter the number of nests lost that day. It helps the eye catch these losses in a large and intricate table if conspicuous red marks are made in the body of the table at points when losses are believed to have occurred. The totals for the columns show the distribution of mortality by days.

SUMMARY

In field studies of nesting birds, many nests are not found at the very beginning or are not followed to a conclusion. When nests are not under observation for their full duration, the observed loss rates are less than the actual rates of the species. The amount of error varies according to the total exposure of all nests not spanned by human observation in the sample. A way of incorporating the time span of observations is to measure the exposure in nest-days, and calculate mortality and survival rates in these units at each stage of the nesting cycle. This method allows pieces of data to be used that would be discarded in customary analyses. A suggested worksheet simplifies analysis, and illustrations answer some questions that troubled users of this method.

ACKNOWLEDGMENTS

David B. Peakall and Clara Dixon were kind enough to read and comment on an earlier draft of this paper.

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OIL THREAT TO AQUATIC BIRDS ALONG THE YUKON COAST

Kees Vermeer and Gary G. Anweiler

Major oil exploratory activities are planned for the Beaufort Sea (Petroleum and Natural Gas Department 1973). Permission already has been granted to AMOCO Canada, a designated operator for a group of oil companies, including Gulf Canada, Hudson's Bay Oil and Gas, and Mobil Oil, to drill an exploratory well on Herschel Island in 1976. Herschel, a former whaling and Royal Canadian Mounted Police station situated on the east coast of Herschel Island, may develop into the major oil exploration and shipping port in the Canadian Sector of the Beaufort Sea (Barry 1970). Since the oil exploration activities may pose a threat to the aquatic birds in the area, we conducted surveys along the Yukon coast for further information on late summer and fall concentrations of birds at sea.

METHODS AND DESCRIPTION OF THE AREA

From 1 August to 21 September, 1973 we conducted a survey of bird occurrence on the beaches and coastal waters of the Yukon Territory (Fig. 1). The survey was divided into 2 phases. Aerial surveys of the entire coastline were flown at intervals and ground observations were made at Herschel Island, where a camp was maintained from 1 August to 8 September. Weather was a limiting factor in this study. Fog occurred frequently and often so unexpectedly that on several occasions an aerial survey had to be discontinued. The fog was often so dense that even ground observations could not be carried out. Surveys were flown in a Cessna 185 float plane from Inuvik, Northwest Territories, during various times of the day depending on visibility and availability of aircraft. An average height of 60 m and air speeds varying from 110 to 190 km per hour were used, depending on visibility and number of birds encountered. A single transect approximately 0.2 km from the coast was flown to count the birds within approximately a 0.4 km wide transect along the coast. Where additional features such as islands and bays were encountered as many additional circuits as needed to cover the enclosed waters and shores were made. One observer was present making observations assisted by the pilot who pointed out flocks of birds.

Ground observations of aquatic birds were made from the base of Avadlek Spit to 1.6 km east of Lopez Point along the south shore of Herschel Island (Fig. 1). Counts were made between 22:00 and 23:00 because then the majority of birds were roosting on the beaches, having returned from between Herschel Island and the mainland. When the water was glassy-calm, birds could be counted over three-quarters of the bay area from a vantage point on a hill on the south side of the island using a 20 × spotting scope. This method combined with aerial surveys of the birds between Herschel Island and the mainland also provided an estimate of the total number of birds present.

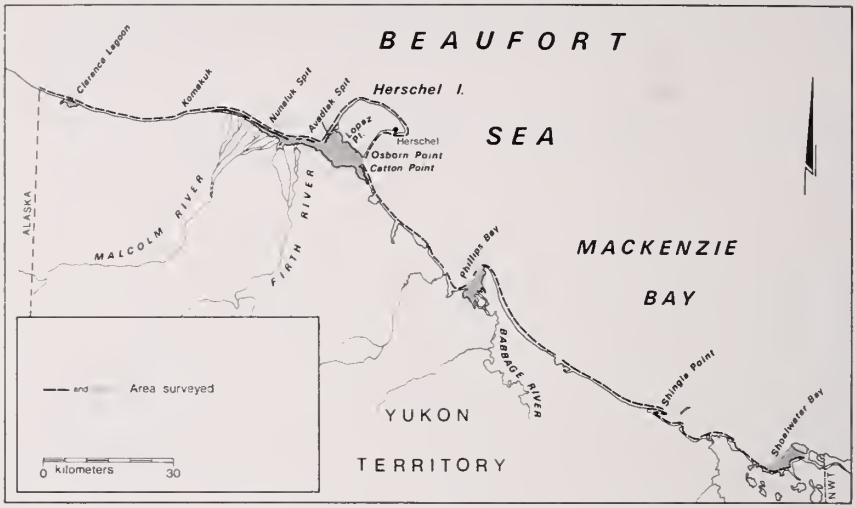

FIG. 1. Yukon coast showing 1973 aerial survey routes.

Some data on bird migration were also obtained during aerial surveys and by watching from various vantage points on Herschel Island.

Much of the Yukon coast is rather barren, with low bluffs abruptly dropping down to a narrow gravel beach. All but the south shore of Herschel Island (size: 115 km^2; highest altitude: 180 m) is of this type of habitat except that the bluffs tend to be higher and the gravel beach is non-existent. The mud bluffs drop directly into the sea.

Where rivers flow into the ocean bays, mud bars and sandspits are often present. This is the case with the Blow River where it enters Shoalwater Bay on the western end of the Mackenzie Delta, with the Babbage River at Phillips Bay, with the Firth and Malcolm rivers at the coast south of Herschel Island, and with several smaller rivers entering Clarence Lagoon. These places are favored by migrating brant (*Branta bernicla* or *B. nigricans*) and smaller numbers of other species such as Glaucous Gulls (*Larus hyperboreus*), phalaropes (mostly *Lobipes*), scaup (*Aythya* sp.), and Red-breasted Mergansers (*Mergus serrator*). Whistling Swans (*Olor columbianus*) and Pintails (*Anas acuta*) frequently occur on freshwater ponds near the shoreline and occasionally on the brackish and salt waters nearby.

With the exception of a few ice floes, the sea east of Herschel Island was ice free as far as we could see from a plane. Wind direction determined the amount of ice present west of Herschel Island. After a day or two of southerly winds, the ice would retreat almost out of sight, but would move in again with a northerly wind. The area from west of Komakuk was generally filled with ice. Nowhere was a solid ice cover encountered.

RESULTS

The total number of aquatic birds observed along the Yukon coast during August and September 1973 is shown in Table 1. The sea ducks,

Table 1

Number of Aquatic Birds Observed Along the Yukon Coast, August–September 1973

Species observed	Date of aerial survey					
	August 9, 12	August* 23, 24	August 31, Sept. 1	Sept. 10	Sept. 14	Sept. 21
Ducks						
Oldsquaw	1617	2181	1464	672	978	1910
Surf Scoter	2617	1458	618	353	579	158
Scaup**	140	175	163	77	93	161
Eider sp.***	78	5	226	18	54	221
Red-breasted Merganser	6	0	5	14	58	139
Pintail	26	55	48	6	0	0
American Wigeon (*Anas americana*)	0	7	0	0	0	0
Unidentified ducks	15	0	45	21	8	31
Shorebirds						
Northern Phalarope	2600	300	100	0	30	0
Unidentified shorebirds	65	500	100	10	0	0
Geese						
Brant sp.	125	541	1746	202	22	30
Snow Goose	0	90	260	0	0	24
White-fronted Goose (*Anser albifrons*)	0	47	0	4	0	137
Canada Goose (*Branta canadensis*)	0	0	6	0	0	0
Gulls and Terns						
Glaucous Gull	281	293	475	281	222	401
Arctic Tern	116	28	0	0	0	0
Swans						
Whistling Swan	49	25	29	40	7	19
Loons						
Red-throated Loon	60	14	51	5	4	0
Arctic Loon (*Gavia arctica*)	6	4	3	0	12	4
Common Loon (*Gavia immer*)	2	1	6	1	0	0
Yellow-billed Loon (*Gavia adamsii*)	1	0	0	1	0	0
Small unidentified loons	0	0	0	0	0	3
Jaegers						
Parasitic Jaeger (*Stercorarius parasiticus*)	4	9	1	0	0	0
Long-tailed Jaeger (*Stercorarius longicaudus*)	2	0	0	0	0	0
Cranes						
Sandhill Crane (*Grus canadensis*)	3	2	7	0	0	0

* The area from Osborn Point to the Alaska border was not surveyed at this time.
** Mostly Greater Scaup.
*** Mostly female Common Eiders.

Table 2

Ground Counts of Oldsquaws and Surf Scoters Along the South Side of Herschel Island, August–September, 1973

Date of observation	Number observed	
	Oldsquaws	Surf Scoters
August 2	1285	1500
August 5	1550	3205
August 13	2133	1835
August 15	1901	1640
August 20	2450	740
August 27	749	253
August 28	487	209
August 29	560	9
September 2	190	0
September 4	150	6

such as Oldsquaws (*Clangula hyemalis*), Surf Scoters (*Melanitta perspicillata*), scaup and eiders, presumably mostly Greater Scaup (*Aythya marila*) and Common Eiders (*Somateria mollissima*), were the most numerous seabirds encountered. Large numbers of molting Oldsquaws and Surf Scoters were observed along the shore and in the water south of Herschel Island during the first 3 and 2 weeks of August respectively (Table 2). From ground observations at Herschel Island and aerial surveys of the birds between Herschel Island and the mainland, we estimated that 5500 Oldsquaws and 4500 Surf Scoters concentrated along the south side of Herschel Island during the molt. No such concentrations of sea ducks were noted anywhere else along the Yukon coast. Small numbers of Common Goldeneyes (*Bucephala clangula*), Harlequin Ducks (*Histrionicus histrionicus*), scaup, Common Eiders, and Red-breasted Mergansers were observed with the Oldsquaws and Surf Scoters. Oldsquaws used a wide range of habitat. Small groups were observed far out at sea but the greatest number was found along the beaches and bays. Oldsquaws occurred in the bay near the base of Avadlek Spit, inside the reef barriers off the Firth-Malcolm Delta and inside Catton Point. Surf Scoters were found in concentrations only south of Herschel Island. Surf Scoters started to depart from the waters south of Herschel Island and the Yukon coast as a whole during the latter half of August (Tables 1 and 2) while aerial surveys showed that Oldsquaw numbers did not decline along the Yukon coast during September (Table 1).

We observed small flocks of molting scaup along the coast but found

no concentrations. The maximum number recorded was 175 on the 23, 24 August aerial survey. Numbers fluctuated little throughout the study period, although flocks that had been noted on successive surveys in the same location during August moved, presumably as part of the fall migration. Although fewer than 60 scaup were observed on occasion with the molting birds concentrated along the south side of Herschel Island, more were usually found in sheltered bays along the coast.

Flocks of female eiders were occasionally encountered along the coast during aerial surveys but we observed no concentration or flights. No males were seen. The large numbers that pass through this area (Barry 1968, 1970; Snyder 1957; Thompson and Person 1963) do so farther out at sea. An estimated 35 pairs of Common Eiders nested on the first barrier reef island east of Nunaluk Spit in 1972 (M. A. Gollop, pers. comm.). Kees Vermeer checked the location on 18 July 1973 but found no nests. Six broods of Common Eiders were seen near Avadlek and Nunaluk Spits in 1973.

Large numbers of shorebirds pass chiefly along the mainland coastline (M. A. Gollop, pers. comm.). Only Northern Phalaropes (*Lobipes lobatus*) stopped in their westward migration in large numbers along the south shore of Herschel Island (Fig. 2). Phalaropes fed along the beaches, in the lee of ice floes and on the open waters of the ocean. They preferred sheltered waters such as lagoons on windy days. The build-up of phalaropes at Herschel Island was of short duration (Fig. 2). We believe many more thousands of phalaropes migrated through the area than we saw. About 2.5% of the phalaropes seen were Red Phalaropes (*Phalaropus fulicarius*), the remainder were Northern Phalaropes. Besides phalaropes, thousands of Pectoral Sandpipers (*Calidris melanotos*) were seen moving eastward along the mainland coast at Nunaluk Spit on 9 and 10 August. Thousands of Golden Plovers (*Pluvialis dominica*) were also observed migrating eastward over Avadlek Spit on Herschel Island from 20 to 25 August. An estimated 600 plovers stopped to roost on Avadlek Spit on 20 August. Thousands of Golden Plovers were observed flying eastward over the Yukon North Slope during the latter part of August (M. A. Gollop, pers. comm.) suggesting that the majority of plovers do not pass over Herschel Island. We saw small numbers of Ruddy Turnstones (*Arenaria interpres*), Semipalmated Sandpipers (*Calidris pusilla*), Least Sandpipers (*Calidris minutilla*), Sanderlings (*Calidris alba*), and Long-billed Dowitchers (*Limnodromus scolopaceus*) on or flying over the beaches of southern Herschel Island.

Brant were the geese most frequently seen. They concentrated in the coastal lagoons, on river deltas, and in bays along the coast during migra-

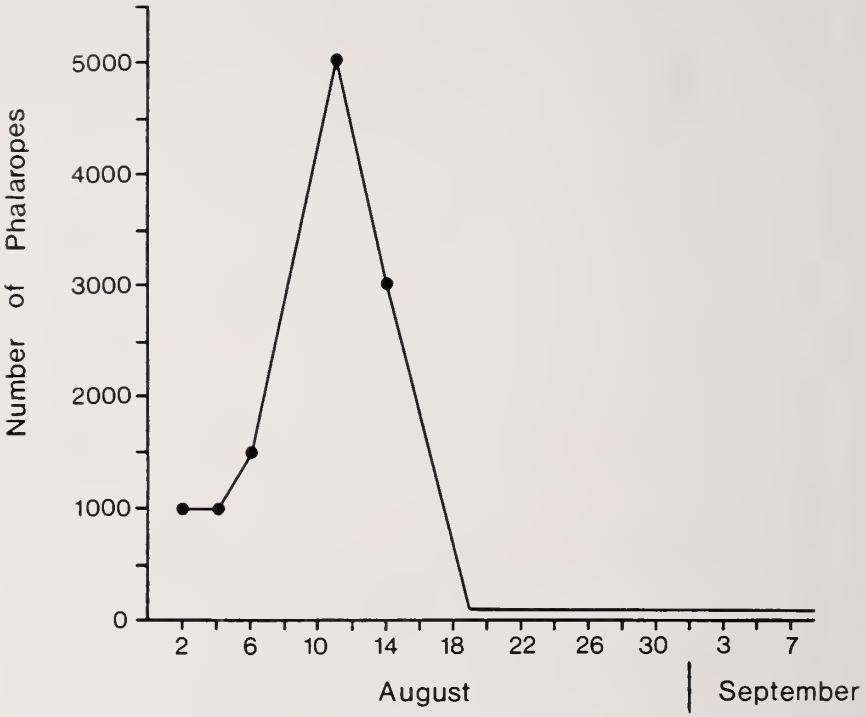

FIG. 2. Ground counts of phalaropes during autumn migration along the south shore of Herschel Island.

tion. The shores and flats of Shoalwater Bay and Phillips Bay, Clarence Lagoon, and especially the area between Nunaluk Spit and the Firth-Malcolm River Delta are used by brant during this time. Brant were observed migrating westward along the mainland from the south side of Herschel Island on 24 (60 birds), 25 (23), and 29 August (45), and on 3 (5 flocks, 235 birds) and 5 September (3 flocks, 160 birds). Most Brant had left the Yukon coast by the third week of September (Table 1).

Hundreds of thousands of Snow Geese (*Chen caerulescens*) use the Yukon North Slope in September (T. W. Barry, pers. comm.) but they generally do not use the marine waters. Snow Geese move mainly along the Yukon North Slope, and rest and feed on the tundra. The only Snow Geese noted on salt water were 90 birds observed on the Firth-Malcolm River Delta on 26 August. Other birds recorded on aerial surveys were birds in flight moving along the coast. The incoming movement of Snow Geese does not appear to follow a well-defined path. Birds appear from

TABLE 3

COMPARISON OF NUMBERS OF AQUATIC BIRDS OBSERVED AT SEA 0.2 KM AND 1.6 KM FROM THE SHORELINE FROM OSBORN PT., NORTH AROUND HERSCHEL ISLAND, TO THE ALASKA BORDER, 1 SEPTEMBER, 1973

Species	Distance at sea from shoreline	
	0.2 km	1.6 km
Red-throated Loon	9	2
Whistling Swan	5	0
Brant sp.	380	0
Canada Goose	4	0
Scaup sp.	15	0
Oldsquaw	386	65
Surf Scoter	300	0
Eider sp.	50	2
Unidentified ducks	30	0
Parasitic Jaeger	1	0
Glaucous Gull	25	5
Total number observed	1105	74

out over the ocean and move southwest onto the Slope. The return migration east to the Mackenzie Delta is mainly over the Slope but in some years the Snow Geese fly back to the Delta over the sea (T. W. Barry, pers. comm.).

Glaucous Gulls, the only gull species noted, were dispersed along the entire Yukon coast. Most gulls were observed near colonies on islands south and southwest of Avadlek Spit, at Phillips Bay, near Shingle Point, and at the settlement of Herschel where offal attracts them. We estimated from aerial observations on 18 July 1973 that approximately 150 pairs were breeding along the Yukon coast. Arctic Terns (*Sterna paradisaea*) also were dispersed along the coast, especially from Herschel Island eastward. The terns departed by the end of August (Table 1). Arctic Terns nested on the island off the tip of Nunaluk Spit in 1972 (M. A. Gollop, pers. comm.).

Whistling Swans were observed on small freshwater ponds along the Yukon coast, especially around Shoalwater and Phillips bays (Table 1). We observed only a few family groups or pairs on brackish or salt water. Their migration followed the coastline but was over land. Although we saw occasional flocks of swans over the sea, we noted none on salt water.

The Red-throated Loon (*Gavia stellata*) was the loon species most frequently observed. Although no visual migration of Red-throated Loons

was observed. their departure from the area is evident from the aerial surveys (Table 1).

On 1 September. while returning from the Alaska border, birds were counted within a .4 km wide transect 1.6 km from land. Only a small fraction of birds was encountered there compared to the numbers seen closer to the coast (Table 3). Frame (1973) reported sighting only 1834 birds over a 550 km cruise in an icebreaker, approximately ranging 50 to 190 km out at sea north of Alaska and the Yukon from 3 to 15 August 1969. The number of 10-min observation periods for 16–64, 65–112, 113–160, and 161–208 km zones from the nearest land were 53, 37, 25, and 37 respectively. The mean number of birds seen per observation period within these zones was 22. 10. 10. and 1 respectively. Bartels (1972) who conducted aerial and boat surveys of sea ducks out to 104 km from the Alaskan north coast during August and September 1971, observed no ducks beyond 56 km. He also reported that 84% of the observed Oldsquaws, the most numerous ducks present, were within 8 km of the shore. From Frame's, Bartels', and our observations it appears that most aquatic birds in the Beaufort Sea are found in the vicinity of the coast during late summer.

DISCUSSION

The Oldsquaws and Surf Scoters appear to be most vulnerable along the Yukon coast to oil pollution because of their molting in concentrations in the barrier-reef protected waters south of Herschel Island. Oldsquaws, scoters and other sea ducks are among the most frequent bird victims of oil pollution in the world's seas (Table 4) because of their presence in heavily navigated sealanes. their large numbers. time spent on the water. and their behavior toward oil slicks. Oldsquaws and scoters dive for food so that when they emerge, they become covered with oil. Oldsquaws sometimes land on oil patches where the deep sea rolls are less heavy (Curry-Lindahl 1960). More than 100.000 Oldsquaws were reported killed by oil discharges from 1952 to 1962 in the Baltic Sea alone (Lemmetyinen 1966). As a consequence of the recurring heavy mortality from oil pollution in the Baltic, the number of Oldsquaws migrating through Finland had been reduced by 1960 to 1/10 the number recorded in the late 1930's (Bergman 1961). Scoters have also been hit hard by oil spills. Goethe (1968) estimated that 500.000 birds. predominantly Black Scoters (*Melanitta nigra*) were killed by the grounding of tanker. *Gerda Maersk*. in northwest Germany. Lemmetyinen (1966) and Joensen (1972) reported approximately 50.000 scoters killed in Baltic and Danish waters from 1962 to 1972 from oil discharges other than from tanker accidents.

Besides sea ducks. alcids are among the most frequent bird victims

TABLE 4

BIRD MORTALITIES RESULTING FROM OIL TANKER ACCIDENTS AND FROM OIL DISCHARGES OTHER THAN TANKER ACCIDENTS IN THE WORLD'S OCEANS AND SEAS

Type of victims	Number of instances reported as predominant victims	Source
Sea ducks (e.g. Oldsquaws, eiders, scoters)	24	Brown et al. (2 instances) 1973, Burnett and Snyder 1954, Goethe 1968, Horwood 1959, Joensen (5 instances) 1972, Lemmetyinen (6 instances) 1966, Marine Pollution Bulletin 1970 1:117, Richardson 1956, Smail et al. 1972, Soikkeli and Virtanen 1972, Swennen and Spaans 1970, Tanis and Mörzer Bruyns (2 instances) 1968, Technical Advisory Committee for oil pollution on the Tay 1968.
Alcids (e.g. murres, razorbills)	12	Aldrich 1938, and Moffitt and Orr 1938, Bourne et al. 1967, Brown et al. (2 instances) 1973, Hope-Jones et al. 1970, Marine Pollution Bulletin 1970 1:117, Richardson 1956, Smail et al. 1972, Tanis and Mörzer Bruyns (2 instances) 1968, Tuck 1960, Wright 1971, Smithsonian Institution Center for Short-lived Phenomena 1971, Card no. 1234–1235.
Diving ducks (e.g. scaups, mergansers)	3	Ranwell and Hewett 1964, Smithsonian Institution Center for Short-lived Phenomena 1970, Card no. 873–874, Vereshchagin 1946.
Shorebirds	2	Harrison and Buck 1967, Ranwell and Hewett 1964.
Grebes	2	Ranwell and Hewett 1964, Smail et al. 1972.
Penguins	2	Westphal and Rowan 1970.

TABLE 4—*Continued*

Type of victims	Number of instances reported as predominant victims	Source
Loons	1	Smithsonian Institution Center for Short-lived Phenomena 1970, Card no. 873 and 874.
Cormorants	1	Smithsonian Institution Center for Short-lived Phenomena 1970, Card no. 873 and 874.
Geese	1	Smithsonian Institution Center for Short-lived Phenomena 1972, Card no. 1372.
Gulls	1	Harrison and Buck 1967.
Gannets	1	Westphal and Rowan 1970.
Fulmars	1	Brown et al. 1973.
Coots	1	Vereshchagin 1946.

of oil pollution in the world (Table 4). Alcid populations in the Yukon, however, are small compared to those in the eastern Canadian Arctic. Only 2 colonies appear to be known in the western Arctic: a colony of fewer than 100 pairs of murres (*Uria* sp.) at Cape Parry, Amundsen Gulf (Barry 1970) and a Black Guillemot (*Cepphus grylle*) colony with some 30 pairs nesting in the mission house at the old Royal Canadian Mounted Police post at Herschel.

Of the shorebirds, the Northern Phalaropes may be most vulnerable to oil pollution along the Yukon coast as they are numerous and feed on the water. However, phalaropes may be less vulnerable to oil than sea ducks because of their relatively short migratory stops.

Of the geese, brant will be vulnerable to oil spills, although to a lesser extent than sea ducks and alcids as they stop only for short periods on Yukon coastal waters. Ouweneel (1971) reported 2000–2500 geese contaminated with oil on their staging areas, the Biesbos and Hollands Diep, in the Netherlands after a spill of 9000 metric tons of fuel oil. Species soiled with oil were Greylag Geese (*Anser anser*), White-fronted Geese, Barnacle Geese (*Branta leucopsis*) and Bean Geese (*Anser fabalis*). Only 23 geese were found dead but the total number killed is unknown due to the departure of the birds from the area. The Smithsonian Institution

(1972) reported that 1000 Pink-footed Geese (*Anser brachyrhynchus*) arriving during migration from Iceland at Invergordon, Scotland, became contaminated with oil after 30 (unspecified) tons of fuel were spilled from a leaky valve during unloading. However, none of the geese, which were roosting in a shallow bay at the time of the spill, were found dead. In the autumn of 1963, the world's population of Greater Snow Geese (*Anser caerulescens atlanticus*) was threatened with pollution as oil dumped into the St. Lawrence had drifted onto the marshes where the birds reside for 2 months. Disaster was avoided by removal and burning of oiled vegetation in the marshes before the geese arrived (Eagles 1964).

Glaucous Gulls, the fifth most numerous species observed along the Yukon coast, will not likely be much affected by oil spills, even though they scavenge most of the summer along the coastline. Gulls can fly over surface pollution and usually have little cause to land in it (Bourne 1968). Moffitt and Orr (1938) reported that gulls escaped major destruction from an oil spill on San Francisco Bay because they feed from the water surface on the wing and rest on the salt water less than diving birds.

The presence of pack ice and the scouring action of ice over the shallow continental shelf of the Yukon may increase the probability of spills resulting from offshore oil exploration, from a possible submarine pipeline connecting Herschel with the mainland, or during oil transfer operations at Pauline Cove. A spill in winter or spring could hinder clean-up operations and large quantities of oil might be trapped beneath the ice (Glaeser and Vance 1971). An oil spill on ice may be covered by falling snow which may make visual detection of its extent impossible and consequently would result in clean-up difficulties (McMinn 1972). Artificial clean-up agents are of little use in winter conditions and oil recovery techniques in the Arctic winter appear to be rapid burning and/or mechanical recovery (Vance 1971, McMinn 1972). Clean-up operations in the summer may be as bad as or worse than in the winter. The relatively low viscosity of oil in summer, may cause it to spread over ice and water. Since there is a lack of, or little, biodegradation in arctic waters (Glaeser and Vance 1971), the oil may be around for a long time and in the absence of clean-up operations could move into lagoons and bays, where it would constitute a threat to molting sea ducks.

The bays bordered by barrier reefs at river mouths along the Yukon coast constitute natural wind-protected havens for molting sea ducks. Oil companies may remove gravel from those reefs to create artificial islands for offshore drilling. Since natural transport of gravel and sediment from North Slope rivers into the Beaufort Sea is slow (Barnes and Reimnitz 1974; Naidu, in press), permanent damage may be done to reefs. A com-

bination of waves, wind, and ice may speed up the erosion of barrier reefs without gravel replenishment and consequently result in destruction of molting areas. If left alone, the reefs may also constitute natural barriers against potential oil spills. Floating boom barriers connecting the reefs south of Herschel Island and along the Malcolm and Firth rivers might keep oil spills, originating elsewhere, out of the most important molting area of Oldsquaws and Surf Scoters along the Yukon coast.

Besides the direct effects of oil, seabirds can be harmed indirectly by contamination of their food supply (primarily marine invertebrates). Marine invertebrates in polar regions grow slowly and development to sexual maturity of certain species may take years (Chia 1970). If an oil spill destroys a marine invertebrate community in the Arctic, replacement will be slow and sea ducks relying on marine invertebrates for food may be forced to leave for other localities where feeding and molting conditions are poor.

SUMMARY

A survey along the Yukon coast in August and September 1973 showed that approximately 5500 Oldsquaws and 4500 Surf Scoters use the reef-barrier-enclosed bay between Herschel Island and the mainland. No other such large sea duck concentrations were observed along the Yukon coast. Oldsquaws and Surf Scoters will be the most likely victims of potential oil spills because of their concentrations, long molting periods, reaction to spills, and nearness to expected oil exploration activities. Large numbers of brant and Northern Phalaropes, which stop during migration in coastal lagoons and river deltas, will also be vulnerable to oil pollution, although to a lesser extent than the sea ducks, because of their relatively short migratory stops.

ACKNOWLEDGMENTS

The authors wish to express their appreciation to M. A. Gollop of L. G. L. Limited, Environmental Research Associates, for useful information.

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GEOGRAPHIC AND ECOLOGICAL VARIATION IN THE FAMILY ICTERIDAE

Peter E. Lowther

The passerine family Icteridae, restricted to but ranging throughout the New World, includes oropendolas, caciques, orioles, blackbirds, meadowlarks, grackles, and cowbirds. The family comprises 95 species placed in 23 genera (Blake 1968; Short 1968, 1969). Comparison of various aspects of the biology of members of such a diverse group may suggest patterns in the evolution of ecological adaptations. These patterns, in turn, may facilitate an analysis of part of the mechanism of adaptive radiation. In this paper I examine variation in size, ecological requirements, breeding biology, and behavior within the Icteridae and suggest explanations for the trends and relationships observed.

METHODS

Aspects of the distribution and biology of all species were determined from the literature, insofar as it was possible, and a list of the 95 species and their attributes is given in Appendix 1. Species density was found by laying a grid with squares representing 259,000 km^2 over maps of species' breeding distributions and finding the number of species occurring within each grid square. After this, geographic distribution of species was simplified for analysis by considering only their latitudinal distribution, for which 30 latitude-sectors were used. These latitude-sectors are 4.64° latitude in width, the same as the north-south side of the 259,000 km^2 grid.

General vegetation types are influenced greatly by climate, and climates, because of the angle of solar radiation to the earth's surface and stable atmospheric circulation, have regular distributions. Particularly, North and South America have, in a general way, similar climates and vegetation types at equal distances from the equator (Fig. 1). Because of this "symmetry" of climate and vegetation about the equator, for statistical tests I combined those species occurring in latitude-sectors equal distances from the equator, on the assumption that they would be influenced by similar environmental pressures.

Statistical analyses used in this paper were 2 × 2 contingency tables, to test associations, and rank correlations, to test for trends with latitude and range size. A description of these statistical methods and appropriate tables can be found in Conover (1971).

The following "definitions" were used in categorizing species:

Latitude.—Species are either "tropical" (center of range within 20° of the equator) or "temperate" (center of range farther than 20° from the equator).

Habitat preference.—Preferred breeding habitat of each species may be "forest", "edge", "scrub", "grassland", "marsh", or "island". *Forest* is used to indicate species of the forest interior. *Edge* indicates species described as inhabiting "open woods", "forest borders", "thickets", "brushy second growth", and "ecotones" or "edges". *Scrub* refers to birds of the more arid edge habitats. *Grasslands* includes birds of the prairie

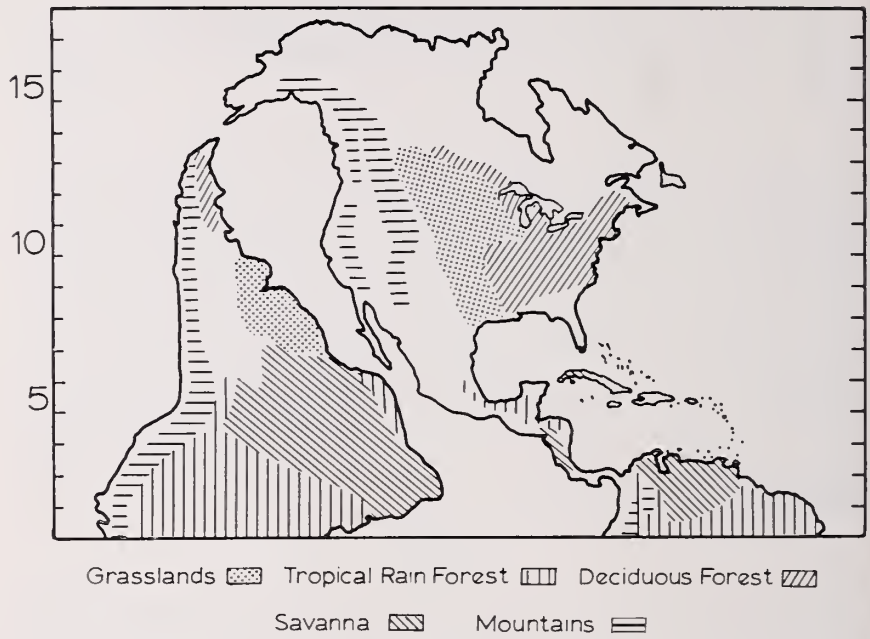


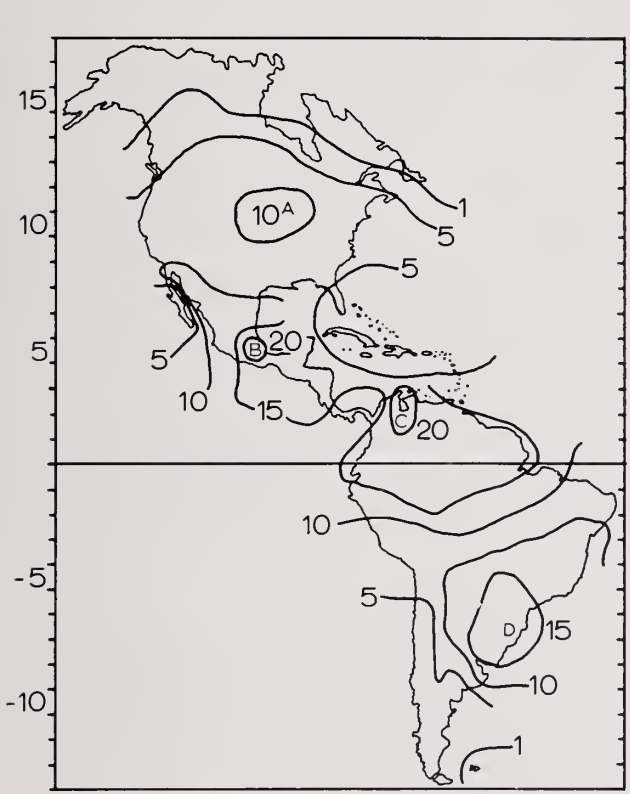
FIG. 1. Distribution of certain vegetation types. This presentation is used to emphasize that similar vegetation types occur equal distances from the equator. East is to the right. Latitude-sectors are indicated on the left. Vegetation distribution is after Küchler (1960).

and pampas regions, "fields", "pastures", and other open grassy habitats. *Marsh* indicates species nesting primarily in marsh and marsh-like habitats. *Island* is used to indicate those species restricted to islands of the West Indies. These habitat classes are also lumped into "woods"—including forest, edge, and scrub habitats—and "open" habitats—being comprised of grasslands and marsh.

Migratory behavior.—A species is "migratory" if it migrates either completely (the winter or non-breeding distribution overlapping little, if any, with its breeding distribution), or only partially (the winter distribution contained within the breeding range, but populations of higher latitudes moving to regions closer to the equator). "Non-migrants" show no north-south seasonal change in distribution. In some non-migrants there may be localized movements, such as altitudinal changes, but this is not migration.

Sexual dimorphism.—Sexual size dimorphism is arbitrarily a difference in wing length between males and females of at least 10%. Sexual plumage dimorphism refers to noticeable plumage differences between sexes as indicated by field guide descriptions. I consider species to be sexually monomorphic if neither of these criteria are met.

Mating system.—Mating systems are monogamous or non-monogamous. Monogamous



	A	B
	1	
	1	
	3	
	5	
	9	1
	11	
	12	3
	13	4
	13	3
	15	1
	17	1
	23	3
	35	12
	27	9
	34	5
	35	7
	29	4
	32	10
	31	6
	24	6
	25	6
	24	2
	19	4
	19	4
	18	2
	12	
	4	
	3	2
	2	
	2	

Fig. 2. Species density for breeding distribution of icterids. Isopleths are shown for 1, 5, 10, and 20 species. The 4 regions of greater density are represented as follows: A—midwestern U.S. (10 species); B—Oaxaca, Mexico (20 species); C—northwestern Venezuela (23 species); and D—Uruguay (18 species). Latitude sectors are indicated on the right.

Column A gives the total number of species occurring within the associated latitude sector. Column B gives the number of species whose center of range is included in that sector.

species are those in which a male pairs with a single female for a nesting attempt. Non-monogamous mating systems include those described as polygamous and polybrachygamous ("promiscuous"). In these cases the male has pair bonds with more than one female during a breeding attempt (see Selander 1972:193).

Territory type.—Territory type, or nesting dispersion, is either Type A or Type O. The first is shown by solitary nesting species. Territories of these species are breeding-nesting-feeding territories (type A) of Nice (1943). The second is shown by those colonial nesting species or those with grouped territories. For these species, territories are nesting only (type D) or nesting-breeding (type B) as categorized by Nice.

SPECIES DENSITY

There are 4 regions where species of Icteridae show relatively greater diversity (Fig. 2): midwestern United States, southern Mexico (Oaxaca), northwestern Venezuela, and the region about Uruguay: Beecher (1950) considered this last region to be the center of icterid origins. One association between species density and general vegetation appears obvious. The midwestern U.S. and Uruguay regions are predominantly grassland habitats. The midwestern U.S. is also an area where several icterids are presently expanding their range (Bobolink, *Dolichonyx oryzivorus*; Western Meadowlark, *Sturnella neglecta*: Brewer's Blackbird, *Euphagus cyanocephalus*: Yellow-headed Blackbird, *Xanthocephalus xanthocephalus*; and Brown-headed Cowbird, *Molothrus ater*: De Vos 1964, Mayfield 1965, and Stepney and Power 1973). These are grassland or edge species that are assumed to be expanding their range because the clearing of forested areas for agricultural purposes has increased suitable habitat for them. The other 2 areas of high species abundance cannot be associated with a single vegetation type since there is greater habitat diversity in the grid squares of the areas.

LATITUDINAL TRENDS

More species occur in the tropics than in temperate regions, a pattern that is obviously not related to continental land area (see Fig. 2). While increased diversity in the tropics has been observed for various groups of organisms (e.g., birds, Cook 1969, Tramer 1974; mammals, Simpson 1964, Wilson 1974; reptiles and amphibians, Kiester 1971), no single causal explanation has been generally accepted. One hypothesis is that, since the tropics have had relatively stable environmental conditions for long periods of time, many species were able to evolve. MacArthur and MacArthur (1961) and Tramer (1969) have shown that bird species diversity increases with increasing complexity of vegetation structure, which is true as the tropics are approached. Ricklefs (1973) also indicates that this increase in avian diversity is related to environmental complexity rather than productivity. Thus, the high density of species in midwestern U.S. and Uruguay regions is probably caused by a mosaic of grassland-deciduous forest; the species density in the Oaxaca and Venezuela regions is a result of greater vegetation complexity superimposed on a heterogeneous topography.

Migration.—In seasonal environments, one would expect a greater proportion of migratory species than in non-seasonal environments. It is expected, then, that those species occurring farther from the equator (i.e., those in more seasonal environments) are more likely to be migratory. The very highly significant rank correlation between distance from the equator

TABLE 1

RANK CORRELATION COEFFICIENTS BETWEEN LATITUDE AND POLYTYPISM, LATITUDE AND MIGRATORY BEHAVIOR, AND LATITUDE AND SEXUAL DIMORPHISM

		Rank Correlation	T	Probability
Distance from equator for center of species' range				
Polytypism		0.1818	0.5847	$.9 > p > .5$
Migratory Behavior		0.9598	10.8134	$p < .001$
Sexual Dimorphism:	Size	−0.6748	2.8917	$p < .05$
	Plumage	0.9353	8.3595	$p < .001$
	Either	0.4930	1.7919	$.2 > p > .1$
Distance from equator for whole of species' occurrence				
Sexual Dimorphism:	Size	−0.3070	1.2493	$.4 > p > .2$
	Plumage	0.9816	19.9195	$p < .001$
	Either	−0.3883	1.0981	$.4 > p > .2$

and the proportion of migratory species supports this commonly made observation (see Table 1).

Sexual dimorphism.—No association was found between secondary sexual size and plumage dimorphism ($\chi^2 = 0.009$, $.975 > p > .9$). Each form of sexual dimorphism will therefore be considered separately.

Sexual dimorphism in size.—There is a significant negative rank correlation between the proportion of species that are sexually dimorphic in size and the distance species occur from the equator (Table 1). This trend is also indicated when the data are tested in a 2×2 contingency table ($\chi^2 = 9.97$, $p < .001$).

Selander (1966) has suggested that where interspecific competition exists, sexual dimorphism in size often is not observed, but with less intense interspecific competition pressure, size dimorphism between the sexes is of greater selective advantage and is associated with differential niche use. Thus, size dimorphism is more likely when intersexual competition is of greater energetic consequence. Such a situation may apply to colonial species, since many individuals of a single species live in a relatively restricted area. If this is true, then breeding dispersion may be important in explaining the relationship between latitude and size dimorphism because colonial species (Type O territories), show size dimorphism ($\chi^2 = 21.58$, $p < .001$), and tend to be tropical ($\chi^2 = 5.35$, $p < .05$).

Sexual dimorphism in plumage.—A highly significant positive rank correlation exists between latitude and the proportion of species showing

plumage dimorphism (Table 1). That is, there is a greater occurrence of plumage dimorphism toward the higher latitudes. Hamilton (1961)—comparing tropical and North American *Icterus*—provided an hypothesis to explain this trend. He noted that those species farthest from the equator were generally migratory and were also frequently dimorphic in plumage. Since males show intense agonistic behavior during the breeding season, females resembling males would cause increased intersexual aggression and result in longer time required for pair formation. Migratory temperate species have a relatively shorter breeding season than tropical species and as a result, Hamilton expected plumage dimorphism to be important in reducing agonistic encounters between male and female and to shorten the time required for pair formation. I tested for association between migratory behavior and plumage dimorphism and confirmed that migratory species do tend to be sexually dimorphic in plumage ($\chi^2 = 12.24$, $p < .001$).

ECOLOGICAL TRENDS

Sexual dimorphism in relation to habitat.—With 5 habitat classes the association between sexual dimorphism and habitat preference is significant for both size dimorphism ($\chi^2 = 11.38$, $p < .05$, $df = 4$) and plumage dimorphism ($\chi^2 = 16.28$, $p < .01$, $df = 4$). Here 3 observations are noteworthy: (1) size dimorphism between the sexes occurs more frequently in forest species; (2) forest species do not show expected frequency of plumage dimorphism; and (3) marsh species tend to show plumage dimorphism. This is partly an artifact of the classification used here—those species classified as forest birds were also restricted to the tropics. When categories were lumped to produce "woods" and "open" habitat sets, I found no association between size dimorphism and habitat ($\chi^2 = 1.78$, $.5 > p > .1$), but there was a significant association between plumage dimorphism and habitat ($\chi^2 = 9.36$, $p < .001$). This association may be partly related to increased visual importance of male display in territorial and reproductive behavior. Among North American icterids, the "song spread" display of several open habitat and edge species has a striking visual component associated with territorial song (see Nero 1963). The orioles, *Icterus* sp., which inhabit more wooded environments, do not have such well developed displays accompanying their song (Skutch 1954, Bent 1958). These displays can be seen from greater distances in exposed habitats and are more appropriate for open habitats in a functional sense.

Mating systems and territory type.—Selander (1972) points out that sexual dimorphism in size is frequently associated with non-monogamous mating systems. I found this to be true for the Icteridae ($\chi^2 = 23.88$, $p < .001$). Selander discusses this further in terms of sexual selection with

size dimorphism being one consequence. In polygamous species there is increased sexual selection among males to show greater dominance (= fitness) and to mate with females. This competition for optimum territories and for females is accomplished through dominance established by larger size in males. Icterid displays often emphasize size by ruffling body feathers (e.g., "song spread"). Colonial species are also likely to be sexually dimorphic in size ($\chi^2 = 21.58$, $p < .001$). Mating systems and territory type are themselves significantly associated ($\chi^2 = 21.36$, $p < .001$)—colonial species tend to be non-monogamous.

I did not find that polygamy is associated with open habitats ($\chi^2 = 1.99$, $.5 > p > .1$), as Verner and Willson (1966) concluded, but their habitat classification differed from mine. In their view, polygamy can evolve if a female that mates with an already mated male with a territory of good quality has an advantage over one mating with an unmated male occupying poorer quality territory. Orians (1969) further developed this model. In marshes, where many polygamous icterids breed, productivity distribution is highly variable, a factor that is considered an important prerequisite for the development of polygamy.

TRENDS RELATED TO RANGE SIZE

Polytypism.—There seems to be no pattern in the latitudinal distribution of polytypic species (Table 1) and I find it impossible to hypothesize about geographic characteristics favoring speciation. Comparison of the size of mean breeding ranges of polytypic and monotypic species showed that the gross breeding ranges of polytypic species are about 2½ times larger than those of monotypic species (3,700,000 km² compared to 1,400,000 km²). Rank correlation between range size and average number of subspecies for each range size class gave a significant association (rho = 0.71, $p \leq .05$). Using the number of named subspecies as a rough measure of the amount of differentiation within a species, I found that widely distributed species are more differentiated. There was no significant association between general habitat types and polytypism ($\chi^2 = 3.13$, $.1 > p > .05$).

Other trends with range size. In addition to that with polytypism, I found significant rank correlations for range size and occurrence of migratory behavior (rho = 0.89, $p < .01$) and for range size and occurrence of Type O territories (rho = 0.77, $p < .05$). The first of these should be related to latitudinal occurrence, but I found no association between latitude and range size ($\chi^2 = 0.52$, $.5 > p > .1$). Instead migratory behavior may be related to continental land area per latitude sector: there is greater land area per latitude sector in temperate North America where most migratory species occur. The relationships between range size and both territory

type and mating system is obscure and I can suggest no explanation for them.

SUMMARY AND CONCLUSIONS

Morphological variation within Icteridae (in the form of sexual dimorphism) may be best explained as results of 2 types of selection. Intersexual competition is the selective force behind sexual dimorphism in size and epigamic sexual selection is the cause of plumage dimorphism.

Neither size dimorphism nor plumage dimorphism show significant associations directly with any of the remaining 7 aspects of biology examined in this analysis except latitude. Plumage dimorphism is more common within the family at higher latitudes; size dimorphism more commonly occurs at lower latitudes. My results are in agreement with Hamilton's (1961) explanation for plumage dimorphism and also offer some support for Selander's (1966, 1972) observations on size dimorphism.

ACKNOWLEDGMENTS

I would like to thank especially Professor R. F. Johnston for his encouragement, helpful discussions and criticisms throughout the development of this paper. At various stages the following people have read, discussed and offered helpful criticism of the paper: Drs. R. S. Hoffmann, N. A. Slade, and R. M. Mengel; also C. L. Cink, K. S. Harris, J. W. Koeppl, D. M. Mortimer, E. C. Murphy, J. W. Parker, and J. D. Robins. For all of this aid I am greatly appreciative.

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Appendix 1. Characteristics of the Icteridae

The classification follows Blake (1968) and Short (1968, 1969) where information on number of subspecies, center of range, range size, and migratory behavior were also obtained. Other sources for this information: American Ornithologists' Union (1957), Beecher (1950), Bond (1971), Friedmann (1929), Meyer de Schauensee (1966), Peterson and Chalif (1973), and Robbins et al. (1966).

Center of range is shown as the latitude-sector north (+) or south (−) of the equator in which the center of a species' breeding distribution occurs.

Range size is divided into 8 classes: 1 (very restricted; type locality only or small islands), 2 (to 3.50×10^6 km^2), 3 (to 10.00×10^6 km^2), 4 (to 16.50×10^6 km^2), 5 (to 32.50×10^6 km^2), 6 (to 65.00×10^6 km^2), 7 (to 97.25×10^6 km^2), and 8 (to 120.00×10^6 km^2). A 5+ indicates range is larger than 25.03×10^6 km^2, the mean range size. Range sizes were determined by measurements of mapped breeding distributions using a compensating polar planimeter.

Migratory behavior is indicated by M for migratory species, P for partial migrants, and n for non-migrants.

Habitats indicated are forest (F), edge (E), scrub (S), grassland (G), marsh (M), and island (I). Sources: Bond (1971), Davis (1972), De Vos (1964), Edwards (1972), Erskine (1971), ffrench (1973), Karr (1971), Meyer de Schauensee (1964, 1970), Monroe (1968), Peterson and Chalif (1973), and Terborgh (1971).

For size dimorphism the percent that female wing length is smaller than male wing length is given. Sources: ffrench (1973), Friedmann (1929), Parkes (1966, 1970), Phelps and Aveledo (1966), Ridgway (1902), and Sclater (1886). S is used to show size dimorphism of 10% or greater if judged by field guide descriptions to be adequate for the criterion used and wing length measurements could not be found.

Plumage dimorphism is indicated by P. No sexual dimorphism in plumage is shown by n. (Sources used are those listed above.)

Mating systems were classified as monogamous (M) or non-monogamous (P); territory type is either Type A or Type O (see text). Lack (1968) and Orians (1972) summarize and provide references for information on mating systems and territory types in Icteridae.

Column headings are (1) Species, (2) Number of subspecies, (3) Center of range, (4) Range size class, (5) Migratory behavior, (6) Habitat, (7) Plumage dimorphism, (8) Size dimorphism, (9) Mating system, and (10) Territory type.

(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)	(10)
Psarocolius									
oseryi	1	−3	3	n	F	n	30%	–	–
latirostris	1	−1	3	n	F	n	35%	–	–
decumanus	4	−2	8	n	E	n	28%	P	O
viridis	1	−1	6	n	F	n	27%	–	O
atrovirens	1	−4	2	n	F	n	S	–	–
angustifrons	7	−1	5+	n	F	n	15%	P	O
wagleri	2	+3	4	n	E	n	29%	P	O
montezuma	1	+4	3	n	E	n	25%	P	O
cassini	1	+1	2	n	F	n	S	–	–
bifasciatus	1	−1	3	n	F	n	S	–	–

Appendix 1. (continued)

(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)	(10)
guatimozinus	1	+2	2	n	E	n	23%	–	–
yuracares	2	−1	5	n	F	n	15%	–	–
Cacicus									
cela	3	−1	7	n	E	P	23%	P	O
haemorrhous	2	−2	7	n	E	P	22%	P	O
uropygialis	3	+2	4	n	F	P	12%	M	A
chrysopterus	1	−6	5	n	F	n	n	–	–
koepckeae	1	−3	1	n	F	n	n	–	–
leucorhamphus	2	−2	4	n	F	n	21%	–	–
chrysonotus	1	−4	2	n	F	n	19%	–	–
sclateri	1	−1	2	n	F	n	S	–	–
solitarius	1	−3	7	n	E	n	10%	M	–
melanicterus	1	+5	2	n	F	P	15%	–	–
holosericeus	3	+2	5	n	E	n	10%	M	A
Icterus									
cayanensis	6	−3	8	n	E	n	n	M	A
chrysater	4	+3	4	n	E	n	14%	M	A
nigrogularis	4	+2	5	n	E	n	9%	M	A
leucopteryx	3	+5	1	n	I	n	7%	M	A
auratus	1	+5	2	n	E	P	1%	M	A
mesomelas	4	+3	4	n	E	n	3%	M	A
auricapillus	1	+3	3	n	E	n	n	M	A
graceannae	1	−2	2	n	S	n	n	M	A
xantholemus	1	−1	1	n	–	n	n	M	A
pectoralis	2	+4	3	n	S	n	5%	M	A
gularis	6	+5	3	n	E	n	8%	M	A
pustulatus	6	+4	4	n	E	P	8%	M	A
cucullatus	5	+6	4	M	E	P	5%	M	A
icterus	6	−3	7	n	E	n	6%	M	A
galbula	4	+9	7	M	E	P	7%	M	A
spurius	3	+9	6	M	E	P	6%	M	A
dominicensis	6	+4	4	n	F	n	5%	M	A
wagleri	2	+5	4	n	E	n	7%	M	A
laudabilis	1	+4	1	n	I	P	0%	M	A
bonana	1	+4	1	n	I	n	n	M	A
oberi	1	+4	1	n	I	P	9%	M	A
graduacauda	4	+5	3	M	E	n	5%	M	A
maculialatus	1	+4	2	n	E	P	n	M	A
parisorum	1	+7	5	M	S	P	6%	M	A
Nesopsar									
nigerrimus	1	+5	2	n	I	n	5%	–	–

Appendix 1. (continued)

(1)	(2)	(3)	(4	(5)	(6)	(7)	(8)	(9)	(10)
Xanthopsar									
flavus	1	−7	4	n	M	P	n	–	O
Gymnomystax									
mexicanus	1	+1	6	n	E	n	n	–	–
Xanthocephalus									
xanthocephalus	1	+11	6	M	M	P	19%	P	O
Agelaius									
xanthoph-thalmus	1	−2	1	n	M	n	14%	M	–
thilius	3	−7	6	n	M	P	9%	–	–
phoeniceus	23	+10	8	P	M	P	18%	P	O
tricolor	1	+9	2	n	M	P	12%	P	O
icterocephalus	2	+1	5+	n	M	P	12%	–	O
humeralis	1	+6	2	n	M	P	8%	–	–
xanthomus	2	+5	2	n	I	n	10%	M	–
cyanopus	4	−4	6	n	M	P	8%	–	–
ruficapillus	2	−4	6	n	M	P	n	–	–
Sturnella									
militaris	1	−1	6	n	G	P	9%	M	–
superciliaris	1	−6	6	n	G	P	n	M	–
bellicosa	1	−3	3	n	G	P	n	M	–
defilippii	1	−8	3	n	G	P	8%	M	–
loyca	4	−11	4	P	G	P	n	M	–
magna	14	+4	8	P	G	n	10%	P	A
neglecta	1	+10	7	P	G	n	11%	P	A
Pseudoleistes									
guirahuro	1	−6	5	n	G	n	n	–	–
virescens	1	−8	3	n	G	n	n	M	–
Amblyramphus									
holosericeus	1	−7	5	n	M	n	n	–	–
Hypopyrrhus									
pyrohypogaster	1	+2	3	n	E	n	S	–	–
Curaeus									
curaeus	2	−11	4	n	E	P	n	M	–
forbesi	1	−4	3	n	–	P	S	–	–
Gnorimopsar									
chopi	2	−5	6	n	G	n	6%	–	–

Appendix 1. (continued)

(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)	(10)
Oreopsar									
bolivianus	1	−5	2	n	E	n	n	–	–
Lampropsar									
tanagrinus	5	−1	5	n	E	n	S	–	–
Macroagelaius									
subalaris	2	+2	3	n	F	n	S	–	–
Dives									
atroviolacea	1	+6	2	n	I	n	6%	–	–
dives	3	+1	3	n	E	P	11%	M	A
Quiscalus									
mexicanus	8	+5	5+	P	E	P	20%	P	O
major	2	+8	3	P	E	P	22%	P	O
palustris	1	+5	1	n	M	P	22%	–	–
nicaraguensis	1	+3	1	n	M	P	22%	–	–
quiscula	3	+10	6	P	E	P	11%	M	O
niger	7	+5	2	n	I	P	14%	M	–
lugubris	8	+2	3	n	E	P	13%	M	O
Euphagus									
carolinus	2	+13	6	M	E	P	5%	M	A
cyanocephalus	1	+11	6	P	G	P	8%	M	O
Molothrus									
badius	3	−6	5+	n	E	n	5%	M	–
rufoaxillaris	1	−7	5	n	E	n	6%	M	–
bonariensis	7	−4	8	n	G	P	12%	M	–
aeneus	4	+5	4	P	E	P	11%	–	–
ater	3	+10	7	P	E	P	10%	M	–
Scaphidura									
oryzivora	2	−2	8	n	E	P	24%	–	–
Dolichonyx									
oryzivorus	1	+11	6	M	G	P	11%	P	A

Appendix 2. Chi-square Tests of Association. The 2 × 2 Contingency Tables and Chi-square Values are Presented as the Lower Triangle of a Symmetrical Matrix. Significance is Indicated for 1 Degree of Freedom.

	Latitude[1]		Polytypism		Range Size		Habitat		Migratory Behavior		Plumage Dimorphism		Size Dimorphism		Territory Type	
	(a)	(b)	(a)	(b)	(a)	(b)	(a)	(b)	(a)	(b)	(a)	(b)	(a)	(b)	(a)	(b)
Polytypism																
(a) Monotypic	18	29														
(b) Polytypic	15	33														
Chi-square	0.52															
Range Size																
(a) Larger than mean	13	18	9	22												
(b) Smaller than mean	20	44	38	26												
Chi-square	1.05		7.69**													
Habitat																
(a) Open	15	10	15	10	14	11										
(b) Woods	12	47	23	36	17	42										
Chi-square	12.66***		3.13		5.57*											
Migratory Behavior																
(a) Migratory	11	7	5	13	12	6	7	11								
(b) Not migratory	22	55	42	35	19	58	18	48								
Chi-square	6.81**		4.18*		11.70***		0.91									
Plumage Dimorphism																
(a) Present	20	24	19	25	20	24	18	21	15	29						
(b) Absent	13	38	28	23	11	40	7	38	3	48						
Chi-square	4.15*		1.30		6.13*		9.36***		12.24***							
Size Dimorphism																
(a) Present	9	38	21	26	17	30	10	33	10	37	22	25				
(b) Absent	24	24	26	22	14	34	15	26	8	40	22	26				
Chi-square	9.97***		0.85		0.53		1.78		0.33		0.01					
Territory Type																
(a) Type A	6	32	11	27	8	30	10	23	10	28	17	21	7	31		
(b) Type O	8	10	6	12	11	7	7	11	6	12	13	5	15	3		
Chi-square	5.35*		0.11		8.74**		0.39		0.29		3.71		21.58***			
Mating System																
(a) Monogamous	15	31	18	28	13	33	9	30	10	36	24	42	12	34	28	3
(b) Non-monogamous	6	8	5	9	10	4	6	8	7	7	8	6	14	0	3	11
Chi-square	0.49		0.05		8.46**		1.99		4.22*		2.24		23.88***		21.36***	

[1] Latitude: (a) temperate, (b) tropical
* $p < .05$; ** $p < .01$; *** $p < .001$

EFFECTS OF BALD EAGLE TERRITORIALITY ON NESTING OSPREYS

John C. Ogden

Simmons (1951) defined interspecific territoriality as aggressive territorial behavior persistently performed by individuals of a species against individuals of different species. Orians and Willson (1964) and Murray (1971) summarized known examples of interspecific territoriality, particularly by nesting birds, and discussed the possible origin and functions of this behavior. Little attention has been given to documenting the effects of this behavior on nesting success of conflicting species. I studied productivity and factors affecting nesting success in Ospreys (*Pandion haliaetus*) and discovered that Osprey nesting success in my study area was affected by territorial behavior of Bald Eagles (*Haliaeetus leucocephalus*). I also noted that the interspecific relationship between the Ospreys and Bald Eagles differed in some aspects from forms of interspecific territoriality previously described. This paper describes the interspecific territoriality exhibited by Bald Eagles toward Ospreys, and quantifies the effect of this behavior on Osprey nesting success and nest-site selection.

STUDY AREA AND METHODS

Data were collected in Florida Bay, Everglades National Park, Florida. Florida Bay is a shallow estuary approximately 64 by 45 km along its longest east-west and north-south axes, and located at the extreme southern tip of peninsular Florida. The Bay contains approximately 150 small keys (islands), most of which are dominated by mangrove vegetation (Craighead 1971). It is essentially a wilderness ecosystem with little direct human disturbance, having been protected since the late 1940s by the U.S. Fish and Wildlife Service and the U.S. National Park Service. Aerial surveys during the past 10 or more years, primarily by William B. Roberston, Jr., and myself, revealed that some species of fish-eating birds (e.g., Great White Heron, *Ardea herodias occidentalis*, and Bald Eagle) have maintained dynamically stable breeding populations and may be at carrying capacity for the system. Other breeding populations have increased slowly during these years (e.g., Roseate Spoonbill, *Ajaia ajaja*, and Osprey) and may be approaching pre-exploitation numbers.

I studied Ospreys in Florida Bay between 1968 and 1974 as part of a National Park Service effort to understand population dynamics in fish-eating birds. The most intensive field work was conducted on 3 keys in the northwestern Bay (Palm, Frank, and Murray keys) where I closely followed the history of about 55 Osprey nesting sites during the 7 breeding seasons. Every active nest was visited from 1 to 6 times (nests visited 3 or fewer times were usually those that failed early) during each breeding season. I also surveyed by airplane all Osprey nests in the Bay in 1968 and 1973. The Bald Eagles in Florida Bay have been studied each year since 1960 by William B. Robertson, Jr., primarily by means of monthly aerial surveys of nests during each breeding season.

RESULTS

Each pair of Ospreys in the Bay defends only its immediate nest site from other Ospreys. Consequently several nests may be grouped, with individual nests occasionally as close together as 20 m. Most Ospreys in the Bay lay eggs in December or January, and fledge young during March or April (since the nesting season of both these raptors overlaps 2 calendar years, I refer to a particular breeding season by the second year: what I call the 1972 season actually began in late 1971). Food material collected from nests indicated that 3 species of fish, a mullet (*Mugil*), a sea catfish (*Arius*), and a jack (*Caranx*) are the prey most frequently taken by Ospreys in western Florida Bay. Bald Eagles in the Bay exhibit strong intraspecific territoriality. Generally a pair of eagles defended an area at least as large as an entire key, so that there was never more than one nest on a key. The eagles have a breeding schedule similar to Ospreys, laying eggs between late November and January, and fledging young during the spring. Eagles feed on a wide range of fish, birds, and turtles, but the 3 species of fish important to Ospreys appear to also be primary food species for eagles. In February 1973, there were 229 Osprey nests and 25 occupied Bald Eagle nests in Florida Bay.

Ospreys and Bald Eagles in the Bay are constantly in situations where interspecific territorial conflict is possible (I exclude from this discussion the interspecific conflicts where eagles harass Ospreys to steal their fish, as I saw nothing in this behavior to suggest that it related to changes in Osprey nesting). The conflicts I witnessed typically occurred when one or two eagles and one or several Ospreys were soaring over keys where both species nested, or when a perched eagle took flight from near its nest in response to a nearby soaring Osprey. I observed both species as aggressors. The aggressor usually called repeatedly and simultaneously made a shallow diving pass toward the other bird. If the attacked bird was an eagle, it usually either ignored the aggressor Osprey or performed a defensive roll in the air: if the attacked bird was an Osprey, it usually made a brief escape flight.

Eagles were persistently aggressive on keys with active eagle nests, although data presented here indicate that it probably is true that eagles only show persistent aggressiveness toward Ospreys when eagles are nesting at a new site. By contrast, Ospreys were most often observed as aggressors at sites where active Osprey nests were in close proximity to one or a pair of inactive resident eagles. Generally this occurred when an eagle on nesting territory apparently failed to acquire a mate, or a pair of eagles failed early in their nesting attempt but remained on the territory. In these situations Ospreys were not persistently aggressive. Ospreys generally ignored perched eagles, while aerial conflicts often appeared to follow chance encounters rather than

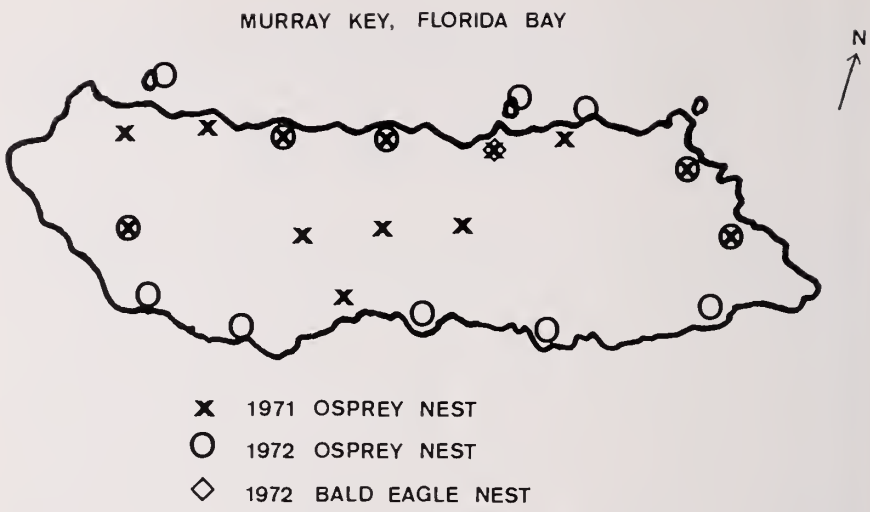

FIG. 1. Location of active Osprey and Bald Eagle nests on Murray Key, Florida Bay, in 1971 and 1972.

result from active territorial display by Ospreys. Thus only the behavior of eagles in the former situation is true interspecific territoriality.

Murray Key.—Interspecific territoriality by eagles apparently caused nearby Ospreys to relocate nests, and resulted in reduced nesting success. These effects are best seen from my observations on Murray Key. Murray is approximately 1010 m long and 375 m wide. Between 1968 and 1973, Murray supported 12 to 14 breeding pairs of Ospreys, but only 9 pairs in 1974. A pair of eagles nested on Murray for at least 11 years through 1968, then moved to nearby Oyster Keys. The eagles returned to Murray in the 1972 season, and nested successfully on the north shore in a nest used in previous years by Ospreys.

The return of these eagles to Murray Key resulted in frequent conflicts with Ospreys. One or both eagles usually were the aggressors, although the occurence of an eagle low over Osprey nests stimulated Ospreys to make occasional flying passes at the eagles. The highest frequency of interspecific activity was observed when I visited the key on 16 December, 4 January, and 19 January, when an eagle chasing an Osprey, or aerial passes by one species toward the other, generally occurred 2 to 4 times per hour throughout each day. This peak activity occurred when the eagle nest contained eggs or small young. I noted interspecific conflicts over most of the key, but primarily along the north shore. The particular attention of the eagles to the north

TABLE 1

REPEAT USE BY OSPREYS OF NESTS ON MURRAY KEY, FLORIDA BAY, 1968 THROUGH 1974

1968 nests active in 1969:	11 of 12	(91%)
1969 nests active in 1970:	12 of 14	(85%)
1970 nests active in 1971:	13 of 13	(100%)
1971 nests active in 1972:	5 of 13	(38%)
1972 nests active in 1973:	9 of 13	(69%)
1973 nests active in 1974:	9 of 12	(75%)

shore resulted in much reduced soaring and general flight activities by Ospreys there.

Correlated with the occurrence of interspecific conflict on Murray Key in 1972, Ospreys relocated 8 of 13 nests and experienced reduced nesting success. The pattern of nest relocation is shown by comparing 1971 nest sites with those for 1972 (Fig. 1). Of the 8 relocated nests, 5 were built on the south shore, away from the eagle nest on the north shore. Three Osprey nests on or near the north shore, however, remained active both years, and the 3 other relocated nests were rebuilt only short distances from the 1971 sites, and not necessarily farther from the 1972 eagle nest. Although the general direction of Osprey nest relocation was away from the eagle nest, no strong correlation exists between the pairs that moved and their closeness to the eagle nest. I do not understand why some pairs moved and others did not, because I did not quantify differences in the way individual Ospreys reacted to the eagles. The significance of 8 relocated Osprey nests in a single year is shown in Table 1, which shows nest changes for each year between 1969 and 1974. Between 69 and 100% of nests used one year were used again the next year, except in 1972 when the eagles returned and the Ospreys reused only 38% of existing nests.

The reduced nesting success on Murray in 1972, compared with preceding years and with 1974, is shown in Table 2. Ospreys experienced even poorer production in 1973, almost certainly due to a local food shortage caused by weather conditions rather than disturbance by eagles. The poor nesting in 1973 was widespread among Ospreys in northwestern Florida Bay as well as among Brown Pelicans (*Pelecanus occidentalis*) and Double-crested Cormorants (*Phalacrocorax auritus*). Reduced Osprey productivity in 1972 was not repeated in 1974, although the eagles nested on Murray in 1973 and 1974. During the 1973 and 1974 nesting seasons I did not observe territorial conflicts between the eagles and Ospreys. It appears the species adjusted to each other after 1972.

Table 2

Osprey Production on Murray, Palm, and Frank Keys, Florida Bay, 1968–1974

	1968	1969	1970	1971	1972	1973	1974
MURRAY KEY							
Active nests[a] (total nests)[b]	11(12)	10(14)	10(13)	11(13)	11(13)	9(12)	6(9)
Successful nests[c]	5	8	6	9	3	0	5
Young fledged	10	13	12	13	4	0	7
Young per active nest	0.90	1.30	1.20	1.18	0.36	—	1.16
PALM KEY							
Active nests (total nests)	25(31)	24(27)	23(29)	25(27)	24(27)	21(28)	20(25)
Successful nests	19	12	9	12	13	1	14
Young fledged	30	20	14	19	17	2	26
Young per active nest	1.20	0.83	0.60	0.76	0.70	0.09	1.30
FRANK KEY							
Active nests (total nests)	15(15)	15(16)	14(17)	19(19)	18(24)	13(18)	12(15)
Successful nests	6	8	8	8	13	4	8
Young fledged	12	12	11	11	20	6	11
Young per active nest	0.80	0.80	0.78	0.57	1.10	0.46	0.91

[a] Nests that definitely received eggs.
[b] Total number of complete nest platforms (same as total number of pairs).
[c] Nests that definitely fledged one or more young.

If the reduced production on Murray in 1972 was eagle-caused and not due to a more widespread phenomenon, then 1972 Osprey production on nearby keys where there was no change in eagle nesting sites should have been more close to normal. This was true for Ospreys on Palm and Frank keys where production was average or above average (Table 2). The small number of young Ospreys produced on all 3 keys in 1973, referred to above, is also shown.

The 4 young Ospreys fledged on Murray in 1972 came from 3 south shore nests, among the Osprey nests farthest from the eagle nest. Although I suggest that territorial behavior by the eagles was the ultimate cause of failure of other Osprey nests on Murray, the precise way this behavior resulted in the nest failures is uncertain. I did not see direct disturbance by the eagles to the Osprey nests. Possible reasons for the nest failures, however, are revealed by a comparison of certain aspects of nesting between Murray and the 2 adjacent keys.

Reduced nesting success on Murray Key in 1972 may have been partly due to relatively late egg-laying that year. About one-half of the Frank and

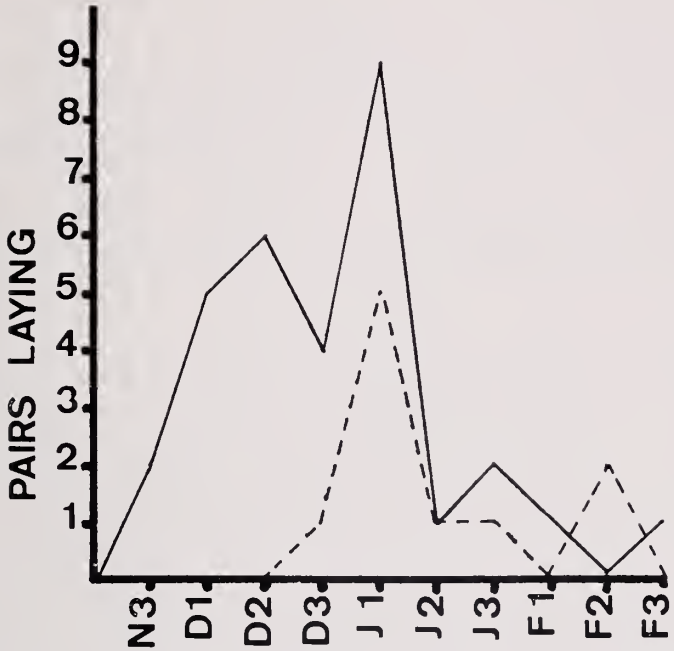

Fig. 2. Number of pairs of Ospreys laying during each one-third month on Palm and Frank keys (solid line) and on Murray Key (dash line), late November 1971 through February 1972.

Palm pairs laid prior to 1 January while only one pair on Murray laid that early (Fig. 2). Osprey eggs laid in December in Florida Bay produce more fledged young per egg than do eggs laid in January. For the years 1971 and 1972 (excluding Murray 1972). 127 December eggs produced 54 fledged young (0.42 young per egg) while 70 January eggs produced 11 fledged young (0.15 young per egg). The reduced productivity from January eggs is partly because the later eggs are more likely to be laid by less experienced, young adult Ospreys. Late eggs may produce fewer young for other reasons also, assuming December is the most favorable time biologically for laying regardless of the experience of the adults. If this is true, the relatively late laying on Murray in 1972 may partly explain the poor production that year. Eggs may have been laid late on Murray because so many nests were relocated. The one nest that received eggs prior to 1 January was a nest used the previous year, and fledged 2 of the 4 young produced in the key in 1972.

The stage at which Murray nests failed is also interesting. The number

Table 3

Osprey Egg and Nestling Losses, Florida Bay, 1972. Compared with Losses in a Maryland Population

Location	Eggs lost	Nestlings lost	Percent egg loss
Murray Key	8	10	44%
Frank-Palm Keys	29	4	87%
Maryland 1963–1969*	745	84	89%

* Reese 1970.

of eggs and nestlings lost from 1972 Osprey nests on the 3 keys is shown in Table 3. I believe the proportion of lost eggs to lost young on Frank and Palm is typical, as is suggested by its similarity to the losses recorded by Reese (1970) in Maryland. The high loss of nestlings on Murray is unusual although I have no certain explanation for their disappearance. It is possible that some were taken by the eagles, especially if Osprey nests were not adequately protected by overly-harassed adults. Eagles will occasionally take nestling Ospreys as was discovered in the Bay by Roberton, who collected the remains of a 5 week old Osprey from an active eagle nest on Manatee Key in 1971.

Remainder of the Bay.—If the relationship between Bald Eagles and Ospreys seen on Murray Key was representative, then similar interspecific territoriality should occur regularly in Florida Bay whenever eagles change nesting sites. To determine if this is so, I looked at the results of the 2 aerial surveys of the Bay in 1968 and 1973, to see if changes in Osprey nest sites correlated with changes in eagle nest sites. The total Osprey nests counted (excluding old, unworked, or incomplete nests) on the surveys was 203 and 229 respectively. My observations in the study area showed that individual pairs did not maintain more than one nest. A count of total nests in the Bay, therefore, provided a close approximation of the number of nesting pairs. I compared the number of Osprey nests on keys that gained, lost, or had no change in eagle nests between the surveys, and found the results consistent with the premise that eagles do influence Osprey nesting. The 6 keys that gained eagle nests showed a cumulative loss of 7 (50%) Osprey nests, while 7 keys that lost eagle nests gained 16 Osprey nests, for a 1973 total nearly 3 times the 1968 total (Table 4). No key that lost an eagle nest also had a loss in total Osprey nests, nor did any key that gained a pair of eagles also show an increase in total Ospreys. On the 6 keys where eagles displaced some Ospreys, I have no information on the timing of Osprey desertions related to arrival of eagles. No Ospreys deserted Murray in 1972, although the number of pairs appeared to have declined during the next 2 years (Table

TABLE 4

COMPARISON OF NUMBERS OF OSPREY NESTS ON FLORIDA BAY KEYS WHERE THERE WAS GAIN OR LOSS IN EAGLE NESTS (1968 VS 1973)

No eagle to yes eagle (N = 6)			Yes eagle to no eagle (N = 7)		
Location	Osprey nest counts (1968–1973)	Years eagles first nested	Location	Osprey nest counts (1968–1973)	Years eagles last nested
Butternut Keys	3–1	1969	Bottle Key	3–5	1968
Roscoe Key	3–2	1969	Bob Keys	0–5	1970
Dump Key	1–0	1970	Jim Foot Key	1–1	1970
S. Pelican Key	3–0	1971	Umbrella Key	1–2	1969
Dildo Key	3–3	1973	N. Pelican Key	2–4	1970
Catfish Key	1–1	1971	Johnson Key	1–3	1971
			Sandy Key	1–5	1971
Totals	14–7			9–25	

2). The number of Ospreys on Palm and Frank also appeared to have declined in 1973 and 1974, where there were no eagle-related reasons for Ospreys to leave. Probably no firm conclusions are possible since the lower nest counts for 1973 and 1974 could be an artifact of generally poor nesting in 1973, and the fact that I made fewer visits to these keys during the 1974 season (22 in 1972 versus 12 in 1974) and could have missed early failing nests.

Table 5 summarizes similar 1968 vs 1973 comparisons for 12 keys that had an eagle nest both years, and for 43 keys that did not have an eagle nest either survey year. Both groups included keys that gained, lost, or maintained the same number of Osprey nests. No pattern of change in Osprey nests occurred in either group, except for modest increases in total nests, reflecting the overall increase in Osprey nests between the surveys.

TABLE 5

COMPARISON OF NUMBERS OF OSPREY NESTS ON FLORIDA BAY KEYS WHERE THERE WAS NO CHANGE IN EAGLE NEST SITES (1968 VS 1973)

Yes eagle to yes eagle (N = 12)		No eagle to no eagle (N = 43)	
1968 Osprey Nests	1973 Osprey Nests	1968 Osprey Nests	1973 Osprey Nests
91	94	89	100
(3 sites no change; 6 sites increased; 3 sites decreased)		(12 sites no change; 20 sites increased; 11 sites decreased)	

DISCUSSION

Murray (1971) categorized forms of interspecific territoriality, including situations where 2 broadly sympatric species with similar habitat requirements are able to co-occupy habitat if the species exhibit different territorial systems. Murray also recognized a different relationship where 2 sympatric species with similar optimum habitats, both strongly territorial, will establish mutually exclusive territories if the species differ in size and the larger displaces the smaller. The former relationship is exemplified by Red-winged and Tricolored blackbirds, *Agelaius phoeniceus* and *A. tricolor* (Orians and Collier 1963), while the second relationship is exemplified by Red-winged and Yellow-headed blackbirds, *Xanthocephalus xanthocephalus* (Orians and Willson 1964). The relationship between Ospreys and Bald Eagles in Florida Bay seems to combine elements of both; the species have different territorial systems, and eagles are decidedly larger than Ospreys. The size difference may contribute to the eagle's dominance over Ospreys, although the fact that Ospreys maintain such small territories probably is more important in allowing the species to co-occupy habitat.

The period of intense territorial activity by eagles is time-limited at any site, apparently because of an adjustment that occurs after eagles initially nest on a key. It probably is true that the overall nesting success by Ospreys in the Bay is dependent on this time-limited characteristic. I saw no territorial behavior directed toward Ospreys by eagles on Palm and Frank keys where eagles nested without interruption during the years of my study, or on Murray Key in 1973 and 1974. And there was no important change in the numbers of Osprey nests between 1968 and 1973 on keys that had nesting eagles throughout those years. I suggest the mechanism that makes possible adjustment between these raptors is that both species exhibit site tenacity and pair fidelity; therefore the complement of Ospreys and eagles on each key is composed largely of birds that were on the same key in previous years. Presumably each pair learns to recognize surrounding pairs, and adjustments made between pairs one year carry through to succeeding years so long as the highly territorial eagles do not shift nest sites.

This paper describes how eagles adversely affect Osprey nesting in certain situations in a region where both species maintain large, healthy populations. I could not help but wonder if there are other situations where Ospreys gain some revenge. Data on Bald Eagle productivity collected by Robertson (pers. comm.) reveal considerable variability in nesting success, with some pairs having poor nesting consistently. I considered the possibility that in some way Ospreys might be responsible for low productivity by some of these eagles. Although the interactions I saw between eagles and Ospreys showed no persistent interspecific territorial behavior by the

Ospreys, it remains possible that reduced nesting success by eagles could occur where a pair is greatly out-numbered by nearby Ospreys (Palm Key had 25 active Osprey nests to 1 eagle nest in some years). Out-numbered eagles might devote an unusually large percentage of their time defending their territory so that other activities are reduced and chances of nesting failure become increased. A reexamination of my observations, however, did not reveal a clear pattern of eagles with poor nesting histories correlated with large numbers or high densities of nesting Ospreys. It seems that Ospreys in the Bay do not regularly cause specific pairs of eagles to have poor nesting, although more intense observations at certain nests might reveal exceptions.

SUMMARY

Bald Eagles in Florida Bay, Everglades National Park, exhibit interspecific territorial behavior toward Ospreys. On Murray Key, an intruder pair of eagles in 1972 resulted in relocation of nest sites by 8 of 13 pairs of Ospreys and reduction in Osprey nesting success. The conflict on Murray was not repeated in years after 1972, and Osprey nesting success improved although the pair of eagles remained. Aerial surveys of the entire Florida Bay showed an increase in numbers of Osprey nests on keys that lost a pair of eagles, and a decline in Osprey nests on keys that gained eagles. I suggest that a pair of eagles only exhibits territorial behavior toward Ospreys in the year when eagles first nest on a key, and that this behavior is not maintained in following years due to adjustments made as pairs learn to recognize adjacent pairs, a process that is possible because of the site tenacity and pair fidelity of both species.

ACKNOWLEDGMENTS

This study was undertaken while I was employed by the Office of Natural Science Studies, U.S. National Park Service. I benefited from discussions of this project with William B. Robertson, Jr., and I thank him for use of some of his Bald Eagle data and for his advice on this paper. Alexander Sprunt, IV, and Richard T. Paul also offered valuable criticisms of the manuscript.

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BREEDING BIOLOGY OF THE GOLDEN EAGLE IN SOUTHWESTERN IDAHO

JOHN J. BEECHAM AND M. N. KOCHERT

In view of population declines in several species of raptors in North America and Europe in the last 25 years (Hickey 1969, Ratcliffe 1970, Cottam 1961), a great need exists for studies that help us ascertain norms in unaffected raptor populations and identify factors contributing to the declines. In this regard, in 1966 the U.S. Bureau of Sport Fisheries and Wildlife (Division of Wildlife Research and Division of Wildlife Services) initiated a study of the Golden Eagle (*Aquila chrysaetos*) in southwestern Idaho and southeastern Oregon. That preliminary field work laid the foundation for a longer-term ecological study of Golden Eagles in southwestern Idaho, the results of which are reported here. In this paper we describe nesting success, density, mortality, and evaluate current population status of Golden Eagles in southwestern Idaho.

During 1968 and 1969 we concentrated on obtaining basic information on food habits, productivity, nesting density, mortality factors, and behavior of Golden Eagles. In 1970 and 1971 our objectives were: 1. to ascertain the reproductive success and density of the breeding population; and 2, to identify certain mortality factors.

STUDY AREA AND METHODS

The principal study area was the Snake River Plain between Bliss and Marsing, Idaho, and encompassed 240 km of the Snake River. Scattered nests along the Boise, Payette, and Weiser rivers, were studied less intensively.

The Snake River Canyon forms the major geologic feature of the area. Basalt and ash cliffs, 8 to 120 m high, plus occasional benches and buttes, provided most of the nesting sites. Sagebrush flats, extending into the foothills of the Sawtooth mountain range to the north and the Owyhee range to the south, border the area and provide adequate hunting areas. Elevation of eagle eyries studied ranged from 700 m along the Snake River to 1525 m in the mountains north of Boise.

The area is in the Upper Sonoran life zone. Dominant species on the flats are sagebrush (*Artemisia tridentata*), rabbitbrush (*Chrysothamnus nauseosus*), shadscale (*Atriplex confertifolia*), and cheatgrass (*Bromus tectorum*). At higher elevations the dominant species are ponderosa pine (*Pinus ponderosa*), bitterbrush (*Purshia tridentata*), and sagebrush. Cottonwood (*Populus* sp.), willow (*Salix* sp.), and golden currant (*Ribes aureus*) occur along the river and creek bottoms. Cultivated lands, which produce largely sugar beets and potatoes, comprise approximately 18% of the study area. The uncultivated portions of the area are grazed by sheep and cattle.

Field work in 1968 began in June and continued through August. A second field season extended from February through August 1969. Field seasons in 1970 and 1971 lasted from mid-March to early September. Division of Wildlife Services maps provided the

locations of many eyries. We also flew over the area in a fixed-wing aircraft in late March and early April each year to locate active nests. Systematic ground searches throughout the nesting season revealed additional active eyries. All active and alternate nest sites were plotted on U.S. Geological Survey maps.

We used standard rapelling gear and techniques to gain access to each eyrie. Productivity and nesting success data were obtained from one visit to an eyrie prior to hatching, several visits during the nestling period, and one visit after fledging. All eaglets were banded with Fish and Wildlife Service bands. Most eaglets were marked with individually color-coded neck markers (Beecham 1970) or color-coded wing markers (Kochert 1972).

Throughout the nesting season we made a special effort to collect and autopsy dead eagles.

RESULTS AND DISCUSSION

Nesting density.—The number of breeding pairs along the Snake River remained relatively stable during the earlier phases of the project: 25 pairs in 1967 (Hickman 1968), 27 in 1968, and 28 in 1969. An increase in the number of pairs occurred in 1970 (40) and in 1971 (56). Only one new site (active and alternate nests used by a breeding pair) was established in 1970, despite the major increase in number of nesting pairs located. The remaining 1970 and 1971 pairs used traditional sites. Lockie and Ratcliffe (1964) observed recolonization of ancestral sites in the Hebrides Islands when nesting density increased. One factor contributing to the increased density that they observed was increased availability of sheep and deer carrion. In our study, peaks in blacktail jackrabbit (*Lepus californicus*) densities in southwestern Idaho in 1970 and 1971 (R. Griffith, pers. comm.) probably contributed to increased numbers of known nesting pairs, but some of the increase may have been artifactual due to our increased knowledge of the study area and better detection of eagles.

The number of alternate nests per nesting site in the area ranged from 1 to 12 (mean = 6). Three pairs in 1970 and 4 in 1971 laid eggs in nests constructed the same year.

The minimum distance between active eyries ranged from 1.9 to 23.3 km in 1969, and from 0.8 to 16 km in 1971. Movement of pairs to alternate nests decreased the minimum distance observed, and discovery of previously unknown breeding pairs was responsible for the increased density. McGahan (1968) in Montana observed Golden Eagles nesting 1.6 to 16.8 km apart. Kochert (1972), using a modification of Ratcliffe's (1962) method, calculated density based on a circle around each nest with a radius of ½ the average distance between eyries. He found an average of 73 km^2 per eyrie for the 56 breeding pairs located in 1971. We found one pair per 8 km of river in 1969 and one pair per 5 km in 1971. Figures computed on a linear-kilometers-of-river basis may be a more realistic measure of density than

Table 1
Clutch Sizes of Golden Eagles in Southwestern Idaho, 1969–1971

Year	N	% of clutches with			Average clutch
		1 egg	2 eggs	3 eggs	
1969	22	5	77	18	2.1
1970	25	12	72	16	2.0
1971	42	7	79	14	2.1

those calculated on a per unit area basis, because of the artificial boundaries used in the latter method. Kochert's (1972) figure of breeding pair density (73 km^2) compares favorably with densities found in Scotland. Lockie (1964) found 13 pairs of Golden Eagles nesting at a density of one pair to 70 km^2: Brown and Watson (1964) reported the average area per pair ranged from 46 to 72 km^2 in 4 different areas in the Scottish highlands. In Montana, McGahan (1968) found one pair per 172 km^2, while Reynolds (1969) mapped an 83 km^2 area used by a pair. Dixon (1937) found an average of one pair to 93 km^2 in California.

Territorial intolerance and availability of nest sites regulated the distribution of breeding pairs along the Snake River. Territorial intolerance appeared to be the less dominant force. We observed that nest sites were widely spaced in areas of poor cliffs, whereas in areas of adequate cliffs, pairs nested in close proximity. Ratcliffe (1962) observed the same pattern with Common Ravens (*Corvus corax*) and Peregrine Falcons (*Falco peregrinus*), with densities apparently a function of the availability of suitable cliffs, up to a point where maximum density was reached.

Nesting success and productivity.—A nesting attempt was defined as the laying of at least one egg and was judged successful if one or more eaglets fledged. Ninety-three of 146 nesting attempts (65%) were successful during the study (61% in 1969, 70% in 1970, and 62% in 1971). Nesting success along the Snake River compares favorably with that in a stable population in eastern Scotland (Lockie et al. 1969) and was far above the 29% reported in a declining population in western Scotland (Lockie and Ratcliffe 1964). Nesting success ranged from 63 to 91% during a 6-year study in Montana (Reynolds 1969).

The average size of 89 clutches was 2.1 eggs (Table 1). Proportions of 1-, 2-, and 3-egg clutches did not change significantly from 1969 to 1971. Similar clutch size and frequency data were obtained by McGahan (1968) and Reynolds (1969) in Montana. We found 4 eggs in an eyrie in 1970, 2 in early April, and 2 more 3 weeks later. The adults deserted the nest, leaving 1 egg destroyed, 1 addled, and 2 fertile; we believe that the last 2 eggs laid were

TABLE 2
PRODUCTION AND NESTING SUCCESS OF GOLDEN EAGLES IN SOUTHWESTERN IDAHO 1969–1971

Year	Young hatched per		Young fledged per		Nesting success
	Successful nest	Nesting attempt	Successful nest	Nesting attempt	%
1969	2.1	1.3	1.4	0.9	61.0
1970	1.7	1.4	1.7	1.2	70.5
1971	1.6	1.1	1.8	1.1	62.2
1969–71	1.8	1.3	1.6	1.1	64.6

fertile. Ray (1928) stated that Golden Eagles seldom renest; however, Dixon (1937) believed that in southern California these birds lay a second clutch. We feel that the 4 eggs above represented 2 separate clutches, based on the interval of their appearance. Either 1 female laid 2 clutches for some unknown reason, or 1 mate died and a new one attempted to nest. Sandeman (1957) and Dixon (1937) reported prompt acquisition of new mates in Golden Eagles, but did not observe this occurring during a single nesting season. During 1969, one pair in our study laid a single egg in each of 2 nests located approximately 3 m apart. Green nesting material and freshly killed marmot (*Marmota flaviventris*) remains were found in the uppermost nest, indicating that the pair may have attempted to incubate in that nest. Both nests were abandoned before we visited them.

Hatching dates ranged from 18 March through 21 April (median 11 April) in 1969; 17 March through 12 May (median 10 April) in 1970; and 23 March through 18 May (median 13 April) in 1971. Weather conditions during April 1970 and 1971 were cooler and wetter than those during April 1969 (data from Dept. Comm. Weather Bureau), possibly accounting for the extension of the hatching period into May during 1970 and 1971.

An average of 1.3 young hatched per nesting attempt, and 1.8 hatched per successful pair during the study. Boeker and Ray (1971) reported an average of 1.5 eaglets hatched per nest during a 6-year study in the central Rockies. In our study, abandonment of nests and infertile, destroyed, and missing eggs decreased hatching success. Weather factors and accidental trampling of eggs by parents caused minor losses.

An average of 1.1 young fledged per nesting attempt, while 1.6 young fledged per successful nest during the study (Table 2). Reynolds (1969) reported 1.1 young fledged per nesting attempt during 6 years of study in Montana.

Mortality.—Causes of mortality in the Golden Eagle have received little study. Brown and Amadon (1968:128) suggested mortality during the nestling stage may claim 25 to 35% of the young. In our study, 41 of 129 (32%) young died before fledging.

Possible heat prostration accounted for the largest number (17) of dead nestlings (41% of the mortality). Five of these eaglets were autopsied and were found in good physical condition. These eaglets were discovered in nests with a western or southern aspect, thus exposed to direct sun during mid- and late afternoon. Nelson (1969:66) suggested this time of day is most critical for nestling survival in exposed nests.

Known instances of fratricide, a source of mortality that appears not to have been specifically observed before in North American Golden Eagles (W. R. Spofford, pers. comm.), resulted in the loss of 3 eaglets. Fourteen other eaglets simply disappeared from the nest, and some may have been victims of fratricide. Sumner (1934) states that fratricide may account for many missing nestlings and Ingram (1959) suggests that fratricide occurs frequently in raptors. Although Brown (1955) states that the fighting instinct in young eaglets ceases after the first few weeks (thereafter the eaglets live together amicably), we found that the fighting instinct probably did not cease. Instead, a dominance relationship developed between eaglets (Beecham 1970). In many instances in southwestern Idaho, this hierarchy expressed itself before the smaller eaglet was killed.

Among the 10 dead fledglings examined, 4 died of trichomoniasis, 2 of impact injuries, 1 was shot, and 3 died from unknown causes. Electrocution, the major cause of mortality in immature birds, killed 12 eagles. Four more immatures died of gunshot wounds, 2 of impact injuries, and 2 of unknown causes. Coon et al. (1970) reported that trauma (impact and shooting) was the major cause of mortality in 76 Bald Eagles (*Haliaeetus leucocephalus*). In our examination of 28 dead immature and adult Golden Eagles, electrocution accounted for 43% of the deaths (all immatures), impact injuries accounted for 21%, and shooting for 11%.

Movement and dispersal.—In the United States, certain populations of Golden Eagles exhibited north-south movements (McGahan 1968, Spofford 1964), while others show no extensive movements (Boeker and Ray 1971, Carnie 1954). On our study area many adult birds remained near nesting territories throughout the year. Morlan Nelson (pers. comm.) reported that adult Golden Eagles have been observed in the vicinity of nesting territories during all months of the year in southwestern Idaho.

Fourteen of 16 banded eaglets recovered during the study were found within 174 km of their natal nests. One bird was found dead near Willows, Glenn Co., California, approximately 644 km southwest of the study area. A

second bird was found dead near Nephi, Juab Co., Utah, 563 km southeast of the study area.

Reported sightings of marked birds provided additional data on movements. Twelve of 14 sightings were made within 80 km of the study area. A 6-month-old bird was sighted approximately 483 km southeast of the area, and a 2-year-old was sighted approximately 507 km northwest. Sightings of marked eagles were made in all months except July.

Our tentative assessment is that dispersal appears to be random from our study area, but more data are needed to confirm this. Lockie and Ratcliffe (1964) suggest that surplus Golden Eagles, both adults and immatures, may live a nomadic existence. Forty-six of 73 (63%) of our observations of single eagles during the nesting season were of immatures. Apparently a large number of immatures range throughout the area, but do not remain in a specific area for any length of time. This large proportion of immature birds during the nesting season suggests that we have a stable population in southwestern Idaho (see Brown and Watson 1964).

CONCLUSIONS

The Snake River canyon in southwestern Idaho probably supports one of the highest densities of Golden Eagles in the United States. High nesting densities and good productivity, as compared to data from other eagle populations that are considered to be stable, indicate that Golden Eagles in southwestern Idaho are experiencing no reproductive difficulties at this time.

Three basic factors appeared to regulate Golden Eagle densities: 1, availability of preferred nesting sites; 2, adequate prey populations within the hunting range; and 3, minimum nesting territory size. We feel that our study area supported a near-maximum number of breeding pairs in 1971. Eagle densities were lowest in areas where suitable cliffs were present but most of the land was cultivated. These data suggest that although native prey species are important as a limiting factor to the population, minimum nesting territory size appears to be the factor limiting a further increase in eagle density. While Ring-necked Pheasants (*Phasianus colchicus*) formed an important part of the food brought to nests by eagles in agricultural areas, jackrabbits and cottontails (*Sylvilagus nuttallii*) still predominated (Kochert 1972, Beecham 1970), suggesting that eagles are dependent on lagomorph populations. The extensive, monocultured irrigation projects (characteristic of Desert Land Entry projects in Idaho) could result in a decrease in lagomorph densities with eagle density also decreasing. Approximately 18% of the land within 8 km of the Snake River was cultivated in 1969. Another 4050 ha of Bureau of Land Management holdings within the study area are scheduled to be cultivated each year for a minimum of 10 years (E. Tilzey, pers. comm.).

Symptoms commonly observed in declining raptor populations affected by chemical contamination (Hickey and Roelle 1969) were not evident in eagles in southwestern Idaho. Our data indicate that the eagle population was stable and reproductively healthy, with an abundance of prey, adequate nesting sites low chemical contamination (Kochert 1972), and low intensity of land use.

SUMMARY

The breeding biology of the Golden Eagle was studied along 240 km of the Snake River canyon, southwestern Idaho, from 1968 to 1971. A density of 1 eyrie per 73 km^2 (56 breeding pairs) was found in 1971, or one pair for every 5.8 km of river. An average of 2.1 eggs were laid per active nest, 1.3 young were hatched, and 1.1 young were fledged from 89 clutches from 1969 to 1971. Nesting success ranged from 61 to 70%. Forty-one of 129 (32%) eaglets died before fledging: 17 from possible heat prostration, 14 disappeared, and 10 from miscellaneous causes (including fratricide). Accounting for the deaths of 28 immature and adult eagles were: electrocution 43% (all immature birds), impact injuries 21%, and shooting 11%. Fourteen of 16 banded eaglets were recovered within 174 km of their natal nests, one from 644 km to the southwest, and one from 563 km to the southeast. A two-year-old bird was sighted 507 km northeast of the area. Dispersal appeared to be random in direction.

ACKNOWLEDGMENTS

This report is a contribution of the Idaho Cooperative Wildlife Research Unit, with cooperation of the U. S. Fish and Wildlife Service, University of Idaho, Idaho Fish and Game Department, and Wildlife Management Institute.

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TABLE 1
CLUTCH SIZE OF MARKED RING-BILLED GULL NESTS ON GRANITE ISLAND, 1973

Week of clutch initiation	Average clutch size		
	A × A	A × B	B × B
2–6 May	6.00 (1)	—	—
7–11 May	3.76 ± 0.83* (17)	—	—
12–16 May	3.49 ± 1.08 (43)	3.67 (3)	—
17–21 May	3.20 ± 1.32 (20)	3.00 ± 0.54 (8)	3.00 (1)
22–26 May	2.61 ± 0.61 (18)	3.00 ± 0.60 (12)	2.00 (1)
27–31 May	1.86 ± 0.69 (7)	2.75 (4)	2.00 (2)
1–5 June	2.29 ± 0.95 (7)	2.20 ± 0.84 (5)	1.67 (3)
6–10 June	2.00 ± 0.71 (5)	2.00 (2)	—
Total	3.14 ± 1.16 (118)	2.85 ± 0.78 (34)	2.00 ± 0.82 (7)

* Standard deviation of the mean (also in Tables 3, 4, and 5).

A × B pairs the only significant difference in any of the parameters was the mean breadth of the third egg. Although my sample size of B × B eggs is too small for statistical comparisons, the means of the parameters show all these eggs were smaller than eggs of the other pair types. Shape index values indicate B × B eggs were shorter and broader than their A × A and A × B counterparts.

For all parameters, successful eggs were numerically, but not significantly, larger than unsuccessful eggs (Table 4). Both successful and unsuccessful eggs of A × A pairs averaged larger than eggs of A × B pairs.

Mature-plumaged pairs which started their clutches on or before the mean date of clutch initiation (17 May) laid larger eggs than pairs which started their clutches after the mean date (Table 5). A similar trend occurred in A × B and B × B pairs. Only differences in egg volumes of early and late starting A × A pairs reach significance.

The differences in the median dates of laying among the 3 groups are reflected in their respective success rates. Eggs laid by mature-plumaged pairs had a hatching success approximately twice that of eggs laid by pairs with one immature-plumaged bird. All eggs of B × B pairs were destroyed by a predator, probably Common Crows (*Corvus brachyrhynchos*), within 2 days after laying of the complete clutch. A × B pairs lost 80% of their eggs to predators.

Table 2

Clutch Size Frequency and Hatching Success of Eggs in Marked Ring-billed Gull Nests, Granite Island, 1973

Clutch size	A × A		A × B		B × B	
	number	H.S.[1]	number	H.S.	number	H.S.
1	7 (5.9)[2]	14.2 (1/7)	2 (5.9)	0.0 (0/2)	2 (28.6)	0.0 (0/2)
2	21 (17.8)	16.7 (7/42)	6 (17.6)	0.0 (0/12)	3 (42.9)	0.0 (0/6)
3	59 (50.0)	62.7 (111/177)	22 (64.7)	31.8 (21/66)	2 (28.6)	0.0 (0/6)
4	20 (16.9)	48.9 (39/80)	3 (8.8)	0.0 (0/12)	—	—
5	3 (2.5)	20.0 (3/15)	1 (2.9)	0.0 (0/5)	—	—
6	7 (5.9)	14.3 (6/42)	—	—	—	—
7	1 (0.9)	0.0 (0/7)	—	—	—	—
Means	3.14 ± 1.16(118)	45.1(167/370)	2.85 ± 0.78(34)	21.6(21/97)	2.00 ± 0.82(7)	0.0 (0/14)

[1] H.S. = hatching success (number of eggs hatched/number laid).
[2] percent of total clutches.

TABLE 3

MEAN LENGTH, BREADTH, VOLUME, AND SHAPE INDEX OF RING-BILLED GULL EGGS, GRANITE ISLAND, 1973

	A × A	A × B	B × B
Length (mm)			
1st egg	60.94 ± 2.88 (55)[1]	59.43 ± 3.23 (22)	56.88 ± 3.27 (5)
2nd egg	59.51 ± 2.23 (55)	59.48 ± 2.75 (22)	55.44 ± 2.04 (4)
3rd egg	59.25 ± 2.60 (55)	59.18 ± 1.93 (22)	57.12 ± 0.95 (2)
Mean	59.90 ± 2.09 (55)	59.36 ± 2.26 (22)	55.85 ± 3.14 (5)
Breadth (mm)			
1st egg	41.94 ± 1.31	42.06 ± 1.38	40.57 ± 0.95
2nd egg	42.31 ± 1.09	41.89 ± 1.18	41.24 ± 0.61
3rd egg	41.83 ± 1.38	41.17 ± 0.94	40.40 ± 0.28
Mean	42.02 ± 1.08	41.70 ± 0.81	40.78 ± 0.78
Volume (cm^3)			
1st egg	52.51 ± 4.37	51.42 ± 3.70	45.83 ± 3.96
2nd egg	52.15 ± 3.51	51.15 ± 4.31	46.13 ± 2.74
3rd egg	50.79 ± 4.35	49.11 ± 3.21	45.58 ± 0.13
Mean	51.81 ± 3.57	50.54 ± 3.02	45.89 ± 2.92
Shape Index			
1st egg	68.96 ± 3.58	71.01 ± 5.27	71.49 ± 4.00
2nd egg	71.19 ± 3.08	70.54 ± 3.08	74.44 ± 2.29
3rd egg	70.71 ± 3.46	69.61 ± 2.06	70.74 ± 1.68
Mean	70.23 ± 2.57	70.34 ± 2.81	72.43 ± 3.29

[1] Number in parentheses is clutch sample size.

DISCUSSION

The overriding trends found in this study were that pairs of Ring-billed Gulls which contained at least one immature-plumaged individual started their nesting activities later in the season and laid smaller eggs which were less likely to hatch than pairs composed of 2 mature-plumaged gulls. The reason for the above differences in Ring-billed Gull biology is unknown (but see Perrins 1970:248). Mills (1973) suggested from his work on Red-billed Gulls that slower maturation of the testes of the young gulls delayed courtship and nesting activities. Pairs with 1 or 2 immature-plumaged Ring-billed Gulls seem to spend more time establishing territories. Though territorial behavior was not studied in detail, I noted that 62% of A × B and B × B pairs nested on the periphery of the Granite Island colony. A similar distribution of Ring-billed Gulls, according to age, was noted by Ludwig (1974). Possibly by the time immature birds are physiologically and behaviorally ready to breed, sites

Table 4

Mean Length, Breadth, Volume, and Shape Index of Successful and Unsuccessful Ring-billed Gull Eggs, Granite Island, 1973

	Successful eggs	Unsuccessful eggs
Length (mm)		
A × A	60.06 ± 2.54 (107)	59.59 ± 2.91 (58)
A × B	59.51 ± 3.00 (21)	59.29 ± 2.52 (45)
Breadth (mm)		
A × A	42.16 ± 1.14	41.77 ± 1.47
A × B	41.79 ± 0.81	41.66 ± 1.38
Volume (cm^3)		
A × A	52.26 ± 3.00	50.99 ± 5.08
A × B	50.88 ± 3.63	50.41 ± 4.00
Shape Index		
A × A	70.33 ± 3.63	70.21 ± 3.26
A × B	70.37 ± 3.40	70.40 ± 3.88

in the center of the colony are filled by adults. Adults may also actively exclude younger birds from the center.

The differences in egg success between mature-plumaged and immature-plumaged pairs can most readily be explained by behavioral differences. I have observed in the Granite Island colony that the most persistant incubators are mature-plumaged pairs. If we accept Drent (1973:294) that experience is interwoven with age, then the smaller eggs of immature-plumaged gulls are likely more susceptible to predation than eggs attended by older birds. My observations on the A × B and B × B pairs suggest that egg predation is an important factor governing success of these groups.

These results generally follow the findings of other workers who have investigated age-specific breeding biology of known-age larids. Of significance is that age-specific differences can be demonstrated from plumage differences in Ring-billed Gulls.

SUMMARY

Nesting pairs of Ring-billed Gulls were visually separated into 3 pair types, based on the plumage of mated individuals. Pairs consisted of either 2 mature-plumaged birds, one mature-plumaged bird and one immature-plumaged bird, or 2 immature-plumaged birds. Aspects of the breeding biology confirmed that mature-plumaged pairs nested earlier, had larger clutches and larger eggs which were more successful than pairs with one or more immature-plumaged individuals.

TABLE 5

MEAN LENGTH, BREADTH, VOLUME, AND SHAPE INDEX OF EARLY AND LATE STARTED RING-BILLED GULL CLUTCHES, GRANITE ISLAND, 1973

	Early-started clutches[1]	Late-started clutches[2]
Length (mm)		
A × A	60.07 ± 2.33 (29)	59.70 ± 1.82 (26)
A × B	59.94 ± 2.20 (11)	58.79 ± 2.27 (11)
B × B	57.65 ± 2.10 (3)	54.20 ± 1.38 (2)
Breadth (mm)		
A × A	42.37 ± 0.94	41.65 ± 1.11
A × B	41.88 ± 0.56	41.53 ± 0.99
B × B	40.71 ± 0.94	40.90 ± 0.50
Volume (cm^3)		
A × A	52.77 ± 3.14	50.73 ± 3.78
A × B	51.45 ± 2.80	49.62 ± 3.07
B × B	46.77 ± 3.33	44.37 ± 1.26
Shape index		
A × A	70.63 ± 3.09	69.78 ± 1.78
A × B	69.94 ± 2.22	70.75 ± 3.36
B × B	70.66 ± 2.33	75.51 ± 2.36

[1] Early-started clutches are those started on or before May 17 for A × A pairs, May 25 for A × B pairs, and May 29 for B × B pairs.

[2] Late-started clutches were begun after May 17 by A × A pairs, May 25 for A × B pairs, and May 29 for B × B pairs.

ACKNOWLEDGMENTS

Financial support for this and related studies on Ring-billed Gulls was obtained from the National Research Council of Canada (A6520). I would like to thank Mr. Ray Trowbridge for allowing me to base field operations at Bonavista. I appreciate the assistance of Mrs. Betty Salo and Ms. Lynn Somppi for preparation of the manuscript.

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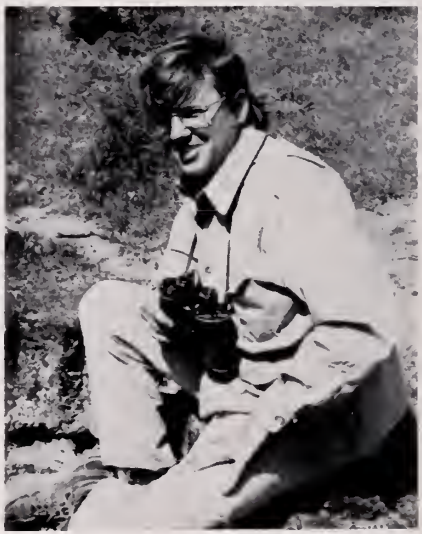

Dr. Thomas C. Dunstan is now a life member of the Wilson Ornithological Society. He is presently Assistant Professor of Biology at Western Illinois University, Macomb, Illinois. Dr. Dunstan's professional interests include radio-telemetry studies on raptorial birds, and he has published a number of papers dealing with Bald Eagles, Ospreys, and Great Horned Owls as well as other raptors. Dr. Dunstan is married and has two children. In addition to his ornithological interests Dr. Dunstan enjoys photography, crosscountry skiing, wilderness camping, and canoeing.

GEOGRAPHIC VARIATION IN WING-LOADING OF THE HOUSE SPARROW

Charles R. Blem

Intraspecific variation in size of widely distributed birds often agrees with modern interpretation of Bergmann's Rule; that is, size is correlated with a combination of climatic variables that includes temperature and/or moisture (James 1968, 1970, Power 1969). Northern races of birds are frequently larger (Mayr 1963:320), but the adaptive significance of increased size has been widely debated (Scholander 1955, Mayr 1956, Salt 1963, Kendeigh 1969, McNab 1971). In general, the word size in ornithological literature refers to wing length, which is often an accurate indicator of body size (James 1970). Wing length varies independently of, or inversely with, body weight in some species (Snow 1958, Hamilton 1961, Rand 1961). Selection for larger body mass without a concomitant increase in wing length could result in conflict between opposing selective forces, particularly in species that depend on flight for foraging or escape from predators. Large birds with relatively small wings will obviously have greater wing-loads and may approach an upper limit at which flying becomes energetically expensive or restricts the ability of the bird to escape predation. In this paper I describe geographic trends in wing-loading in North American populations of the House Sparrow, *Passer domesticus*, and assess the importance of upper limits of wing-loading using data on the flying ability of experimentally loaded birds.

METHODS

Sparrows used in this experiment were captured during winter (November–February) at 11 sites representing a wide latitudinal range (Table 1). Although House Sparrows at northern sites have fewer hours of daylight during the winter for collecting food, they store greater amounts of fat which is necessary for overnight survival (Blem 1973a). Collections were made in late afternoon or early evening and are therefore comparable and representative of birds prepared for surviving a midwinter's night fast.

Chords of both wings of each bird were measured to the nearest 0.1 mm using vernier calipers. Wings were cut off as close to the body as possible and pinned out so that the anterior and proximal edges of the wing were straight and perpendicular to one another. Major wing feathers were positioned in what seemed to be a natural manner and the wing allowed to dry. No shrinkage of the wing occurred with drying. A precise outline was produced by spraying a light layer of paint around the edge of the wing. The area of the resulting silhouette was then determined to the nearest 0.1 cm^2 with a compensating polar planimeter. Subsequent carcass analysis (Blem 1973a) made measurement of wing areas of all birds impossible, so the relationship between wing chord and wing area was determined from measurements of Ohio and Virginia sparrows. The least squares relationship between the average of the chords of both wings and total wing surface

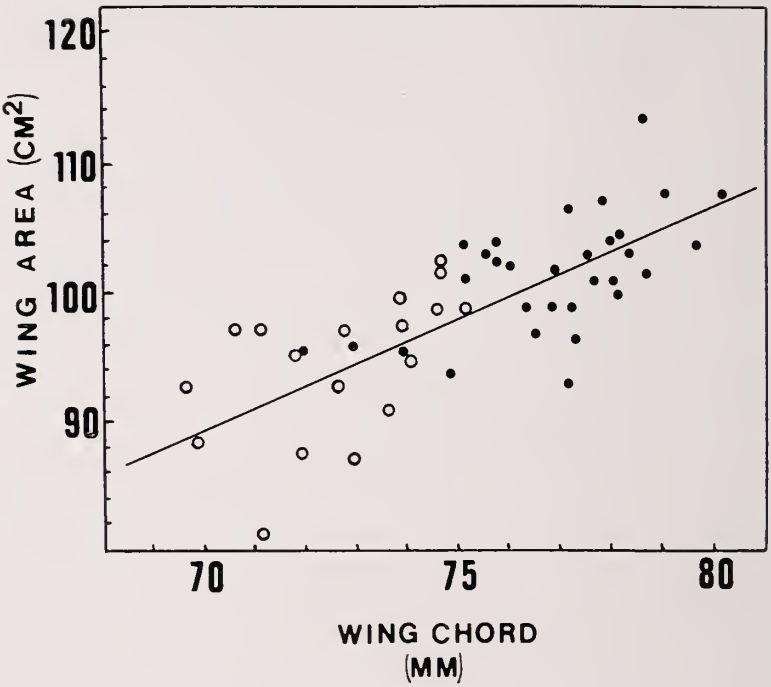

FIG. 1. Relationship between wing area and wing chord in male (●) and female (○) House Sparrows. Wing area (cm^2) = 1.66 wing chord (mm) −25.86 ± 4.07.

is significantly linear and was used to predict wing area in the remainder of the samples (Fig. 1). There is no difference between equations for Ohio and Virginia birds, or between sexes, therefore all data were pooled.

Laboratory tests of the flying ability of artificially weighted sparrows were performed in order to determine the effects of extreme wing-loading and the lower limit at which weight hinders a House Sparrow's flight. Male sparrows freshly caught at Richmond, Virginia were fitted with a harness attached around the neck and body. The harness did not visibly interfere with the flight of any of the sparrows tested. Lead weights were attached to the harness near the keel of the sternum. The locations used were near sites of fat deposition (furcula, lower abdomen, ventral feather tracts) and the center of gravity of the bird. Tests were carried out in a 30 m hallway with 3 m ceilings. Flying ability was subjectively assessed on the basis of altitude of flight, flying time, ability to sustain flight without tiring, and avoidance of capture. Wing-loading was determined after each test from the total weight of bird, harness, and lead weights, and the wing area predicted from the chords of the wings.

RESULTS

Male House Sparrows had significantly different body weight, wing chord, and wing area than females (Table 1). There was a small, but statistically

TABLE 1

MID-WINTER BODY WEIGHT, WING CHORD AND AREA, AND WING-LOAD IN HOUSE SPARROWS

Location (°N. Latitude)	MALES N*	Weight (g)	Wing chord (mm)	Wing area (cm^2)	Wing-load (g/cm^2)	FEMALES N	Weight (g)	Wing chord (mm)	Wing area (cm^2)	Wing-load (g/cm^2)
Churchill, Manitoba (59)	7	33.5**	76.7	101.2	0.332	5	32.7	74.0	96.7	0.339
		±0.5	±0.7	±1.2	±0.003		±1.0	±0.4	±0.7	±0.012
Saskatoon, Saskatchewan (52)	6	34.6	78.6	104.3	0.332	6	32.8	75.5	99.2	0.331
		±0.8	±0.9	±1.5	±0.011		±0.4	±0.5	±0.9	±0.005
St. James, Minnesota (44)	7	32.4	76.9	101.5	0.319	6	31.9	74.5	97.5	0.327
		±0.6	±0.6	±1.0	±0.007		±0.5	±0.7	±1.1	±0.004
Dunkirk, Ohio (41)	11	29.4	77.8	102.6	0.290	4	28.2	72.9	93.9	0.301
		±0.5	±0.5	±1.4	±0.006		±0.6	±0.6	±1.4	±0.008
Monticello, Illinois (40)	12	31.3	78.3	103.8	0.302	13	30.7	75.6	99.4	0.309
		±0.5	±0.4	±0.7	±0.005		±0.4	±0.3	±0.5	±0.004
Columbus, Ohio (40)	6	30.0	77.8	103.7	0.290	4	27.8	72.2	90.5	0.308
		±1.1	±0.4	±2.2	±0.014		±1.3	±0.5	±3.7	±0.010
Plainview, Texas (34)	6	29.2	77.1	101.8	0.287	6	28.3	74.3	97.2	0.292
		±0.4	±0.8	±1.3	±0.006		±0.5	±0.7	±1.2	±0.005
Richmond, Virginia (37.5)	15	28.4	75.9	99.9	0.285	10	28.3	72.9	96.2	0.291
		±0.4	±0.4	±1.0	±0.006		±0.7	±0.7	±1.7	±0.006
Tucson, Arizona (32)	5	26.6	76.8	101.3	0.262	8	27.2	74.7	97.8	0.278
		±0.8	±1.0	±1.7	±0.007		±0.6	±0.6	±1.0	±0.005
Riverside, California (34)	5	28.1	76.4	100.7	0.280	8	27.1	73.2	95.0	0.285
		±0.6	±1.2	±2.0	±0.010		±0.4	±0.4	±0.8	±0.003
Vero Beach, Florida (28)	6	27.7	77.0	101.6	0.272	6	26.5	75.3	98.8	0.269
		±0.4	±0.5	±0.9	±0.003		±0.8	±0.7	±1.1	±0.009

* Sample size.
** Mean ± 1 S.E.

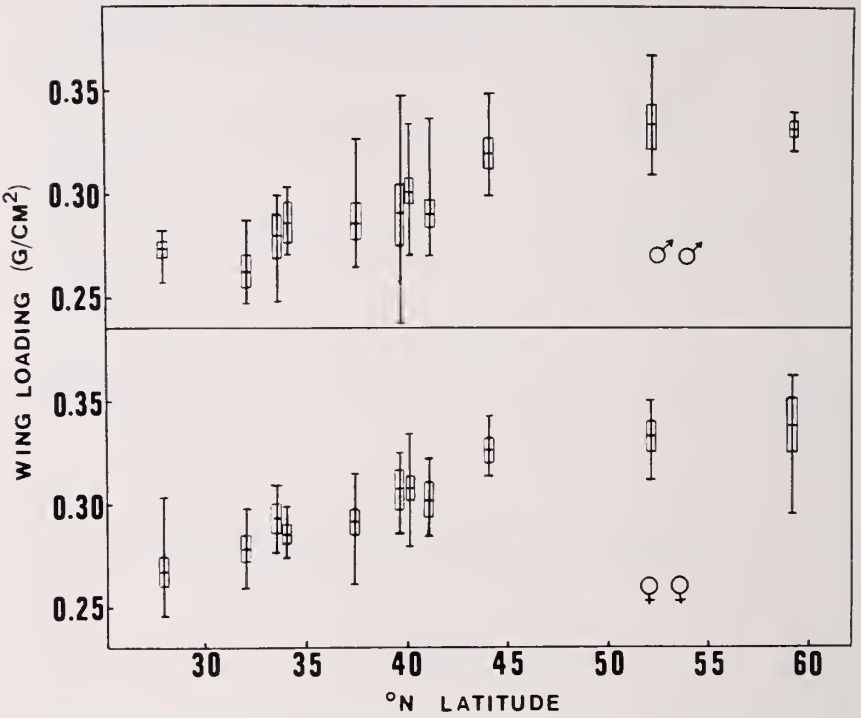

FIG. 2. Wing-loading in House Sparrows in relation to ° N latitude. The vertical line is the range, central horizontal line the mean, and the rectangle represents ± 1 S.E.

significant sexual difference in wing-loading and females had a greater wing-load at 9 of the 11 localities examined. Body weight varies geographically in both sexes and has been discussed elsewhere (Johnston and Selander 1964, Blem 1973a). I found no consistent geographic variation in wing chord or wing area in either sex. Wing-loading increases northward in both sexes, but seems to plateau at the 3 northernmost sites (Fig. 2). Analysis of variance indicates a significant latitudinal effect upon wing-loading in both sexes. The largest sparrow collected during this study, a 37.9 g male from Saskatchewan, also had the greatest wing-load (0.37 g/cm²). Three other sparrows from northern localities were loaded more than 0.35 g/cm². In tests of artificially weighted birds (Table 2), difficulties in flying were first evident in a wing-loading range of 0.33 to 0.35 g/cm². This range is beyond the normal levels of free-living Richmond sparrows, but not that of northern birds. Severe difficulties were usually observed whenever wing-loading exceeded 0.36 g/cm². Although sparrows were loaded up to 0.41 g/cm², no bird failed to take off and all were able to fly at least one length of the test area.

TABLE 2
FLYING ABILITY OF ARTIFICIALLY WEIGHTED MALE HOUSE SPARROWS

Flying ability	Number of birds	Range of wing-loading (g/cm^2)
Natural flight	8	0.26–0.33
Rate of climb visibly impaired, less able to avoid recapture	6	0.33–0.35
Low flight, never able to fly more than 2 lengths of test area before recapture	7	0.36–0.39
Barely able to take off, flight less than 1 m in altitude	5	0.37–0.41

DISCUSSION

Concomitant geographic variation in body weight and wing length can occur several ways. For example, in some species of tits (*Parus*), body weight and wing length increase simultaneously and are correlated with mean temperature of the coldest month (Snow 1954). In the Cardinal (*Cardinalis cardinalis*) there is a trend for increased wing length in the southwestern U.S. and Mexico, while body weight increases northward (Hamilton 1958). Johnston and Selander (1964, 1972, 1973) demonstrated that body weight in House Sparrows varies geographically in accordance with Bergmann's Rule and that wing length clinally increases with latitude and altitude.

If increased body weight is not accompanied by a proportional increase in wing area, it is possible that wing-loading may come into selective conflict with other benefits of increased size, particularly late in each cycle of daily activity when fattening and contents of the digestive tract are at a maximum. Calhoun (1947) demonstrated that average wing length in some U.S. populations of the House Sparrow had increased more than 1 mm between the time of introduction and 1930. This suggests there is selection for increased wing length, although the corresponding changes in body weight are not available.

Wing-loading is not extreme within the area in which the House Sparrow has been long established, but is a potential problem at extreme northern sites (Fig. 2). Blem (1973a) analyzed carcasses of House Sparrows from a wide latitudinal range and found a northward increase in body weight of 6 g. The additional weight consisted of water (48%), fat (31%), lean dry weight (17%), and feathers (4%). Avian races in northern or elevated parts of a species range need to accumulate greater energy reserves for overnight survival because of longer winter nights and or lower ambient temperatures. Greater fat deposits and increased weight of gut contents would result in

heavier wing-loads. Selection might favor increased wing length and/or area to offset such loads and may likewise favor increased mass of breast muscle. House Sparrows at the northern edge of the range are loaded to an extent determined to affect flying ability in laboratory tests. Partial protection from the cold and a nearby food source may allow them to exist here when they might not otherwise. At northern collecting sites, sparrows make extensive use of grain elevators or other protective man-made structures.

There is considerable controversy about the adaptive value of size variation in terms of energetics, but it is possible that some of the wing and body size increases in cooler climates are responses to the necessity for carrying about greater amounts of food in the digestive tract and supporting larger amounts of depot fat. Mathematically eliminating the fat needed to survive cold winter nights reduces wing-loading at northern sites to levels near that of more southerly locations. In addition, increased lean dry weight at northern locales is probably partly composed of increased mass of breast muscle, another adaptation that may be related to carrying greater loads.

Mayr (1956) suggests "multiple solutions for biological needs are the general rule in evolution." Likewise, size gradients may be solutions to multiple needs. Increased size in birds may simultaneously provide better insulation with no relative increase in plumage (Blem 1973b), a relatively greater mechanism for heat production (Blem 1973a), and a solution for increased wing-loading at northern sites.

SUMMARY

Wing-loading of House Sparrows in midwinter increases northward and is greater in females than males. Experimental tests of wing-loading in male House Sparrows indicates that sparrows at northernmost localities may be excessively weighted by increased amounts of fat and water needed to survive long, cold winter nights. Survival may result from their close association with man.

ACKNOWLEDGMENTS

I am indebted to Drs. S. Charles Kendeigh, Richard F. Johnston, and J. F. Pagels for their advice and critical reading of the manuscript, Dr. T. D. Kimbrough, Jr. for loan of equipment and D. W. Spittle for making many of the measurements.

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DEPT. OF BIOLOGY, VIRGINIA COMMONWEALTH UNIV., RICHMOND 23284. ACCEPTED 12 FEB. 1975.

GENERAL NOTES

An optical scope for examining nest contents of tunnel-nesting birds.—Demographic studies of tunnel- or burrow-nesting species have often suffered because devices used to collect data from within nest chambers have been relatively unsophisticated or lacking. We have brought optics into the design of such instruments. While we have used our optical scopes to aid in studies of breeding ecology of 3 tunnel-nesting birds (the Bank Swallow, *Riparia riparia*, and 2 African Bee-eaters, *Merops albicollis* and *M. nubicoides*), we suggest they are adaptable for a wide range of animals.

Analogous scopes, dubbed "Ripariascopes," have been mentioned in the literature (Peterson, Ph.D. thesis, Univ. of Wisconsin, 1953; Svenson, Vår fågelvarld 28:236–240, 1969), but in neither case were lenses employed. Without lenses, resolution of detail is impaired. With the scopes described here, it is possible not only to make egg, hatchling, and early nestling counts, but also to make out such fine details as the presence of small insects within the nest chamber and cracks in eggs. In addition, one can age nestlings because the various stages of feather tract development and pigmentation are easily recognizable.

Basically, the scopes are constructed of aluminum tubing, 25 mm in diameter, which is cut to the desired length. Illumination is provided by two 6-volt, .2 amp, miniature light bulbs (General Electric No. 328) which are mounted at the terminal end of the tube, distal to an elliptical mirror (2 cm × 3 cm) which is set at a 45° angle to the axis of the scope. The end of the tubing is partially cut away to allow light from the bulbs to reach the nest chamber and to be reflected by the mirror back along the axis of the scope to the observer's eye. Wires run from the bulbs along the exterior of the Ripariascope to a 6-volt battery which is suspended from the user's belt. Battery life is prolonged by a switch which activates the lights when desired.

We have built scopes of 2 optical designs. Fig. 1 illustrates a lens system which transmits an image equal in size to the object being viewed. The scope has a length approximately 4 times the focal length (hereafter abbreviated f.l.) of the field lens (lens 3). Hence, by appropriate selection of lenses, a scope of any desired length can be assembled.

Three lenses of the same small (30–55 mm) f.l. and a single longer f.l. field lens are required. Positioning of the lenses is shown in Fig. 1. Lens 1 focuses the image of the nest contents in the plane of lens 2, and lens 3 transfers the image to lens 4, the ocular.

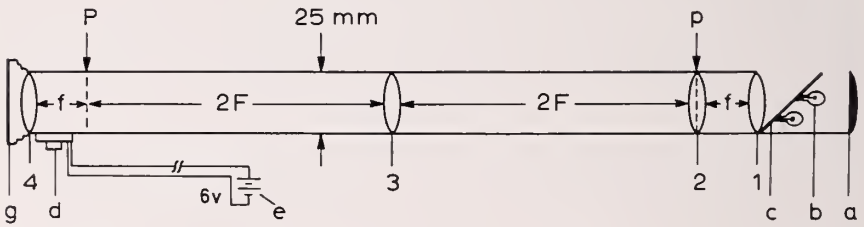

FIG. 1. Generalized Ripariascope lens system. Lenses 1, 2, and 4 are identical lenses of small focal length f (30–55 mm). Lens 3 is the main field lens of focal length F; a = protective endpiece, b = light bulbs, c = mirror, d = switch, e = 6-volt battery, g = rubber eyeguard, p and P = focal plane. Field lenses should be of the achromatic type to insure optical quality.

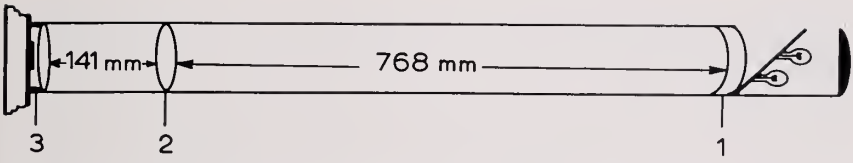

FIG. 2. Design for wide-angle viewing scope: 1 = −17.5-mm f.l. lens, 2 = 120-mm field lens, 3 = 20× eyepiece.

Since the field lens has a f.l. approximately ¼ the scope length, a field lens of f.l. 250 mm is suitable for a 1 m Ripariascope while a 600-mm lens makes a scope 2.4 m long. (Carmine Bee-eaters nest as deep as 3 m).

When looking into large nest chambers or examining large nestlings, it may be desirable to increase the field of view at the expense of magnification. We found a second scope design optimal for these purposes (Fig. 2). It incorporates a wide-angle lens (f.l. = −17.5 mm) as the first lens, a 20 × microscope eyepiece (f.l. = 12.5 mm) as the ocular, and a 120-mm f.l. field lens. The lenses are positioned according to the optical equation for magnification ($m = d_1/d_2 \times f.l._2/f.l._1$) in such a way as to reduce the final image to one-quarter size and increase the field of view 4-fold.

It is possible to extend the length of this one-meter scope by applying the principles illustrated in Fig. 1. For example if a scope of overall length of 1.6 m is required, a 600-mm extension must be added. To do this, position a 150 mm f.l. lens 2 focal lengths (300 mm) beyond where the ocular is located in Fig. 2. The microscope ocular is then mounted another 2 focal lengths away from this field lens.

We advise mounting the ocular lens in its own tuhe, the outer diameter of which matches the inner dimensions of the Ripariascope proper. Sliding adjustment of the ocular then permits accurate focusing. A very long scope will suffer light loss due to extraneous reflections unless the inside of the tuhe is coated with flat black paint. A rubber eyeguard also improves viewing by allowing accommodation of the eye to the light level within the scope. One final tip: we are careful to make the exterior of our scopes as round and smooth as possible. This minimizes the potential damage to a hole that can occur by accidental dislodging of dirt.

Once the nestlings begin to approach full size, the Ripariascope is no longer the optimal instrument. By this time, the entire field of view is filled by only a part of a single nestling's body. At this point, direct visual observation is preferahle and we found that a headlamp held in the hand affords the best manipulation of light for peering down a long hole. With these 2 approaches, one is well-equipped to collect accurate data on all stages of the breeding cycle of tunnel-nesting birds.

We wish to thank James Ahlstrom, Bradford Howland, Robert H. Pohl, and Donald K. Riker for design suggestions.—NATALIE J. DEMONG AND STEPHEN T. EMLEN, *Section of Neurobiology and Behavior, Division of Biological Sciences, Cornell Univ., Ithaca, NY 14853.* *Accepted 26 Feb. 1975.*

American Robin feeds garter snake to its nestlings.—On 14 July 1971, at about 2750 m in the Pike National Forest, Teller Co., Colorado, I heard an unusual commotion in a robin's (*Turdus migratorius*) nest which contained 3 nestlings known to be about 10 days old. When I approached a few minutes after an adult left, I observed 2 of the nestlings simultaneously attempting to swallow a snake which was approximately 25 cm long. There was a 5 to 8 cm loop of the snake's body separating the nestlings' beaks. When I returned 10 min later with my camera, the snake had disappeared.

Since the snake appeared dead and I could not find it when I searched the nest site, I assumed that one of the nestlings swallowed it. The snake's color pattern readily identified it as a garter snake, and the only species occurring above 2438 m in Colorado is the wandering garter snake (*Thamnophis elegans*) (Maslin, Univ. of Colo. Studies, No. 6:47–53, 1959).

There are several reports in the literature of American Robins taking small snakes (Marshall, Bird Lore 23:259–260, 1921; McIntosh, Bird Lore 24:152, 1922; Friedmann, The Cowbirds, 259–260, 1929; Bent, U.S. Natl. Mus. Bull. 196:30, 1949; Davis, Wilson Bull. 81:471, 1969; and Netting, Wilson Bull. 81:471, 1969). Both McIntosh and Friedmann indicate that robins will attempt to feed small snakes to their nestlings: McIntosh reported that a robin nestling was unable to swallow a 25 to 33 cm garter snake, and Friedmann, who placed a 7-day-old Brown-headed Cowbird (*Molothrus ater*) in a robin's nest, observed the nestling swallowing a small garter snake fed by an adult robin. —Merle L. Richmond. *U.S. Fish and Wildlife Service, Denver Wildlife Research Center, Lakewood, CO 80225. Accepted 3 Feb. 1975.*

Chipping Sparrows feeding grit to offspring.—On 20 June 1974 at LaCrosse, Wisconsin, I observed an adult Chipping Sparrow (*Spizella passerina*) land among 4 fledglings in crushed gravel about 3 m from where I stood. The fledglings spaced themselves quadrilaterally around the adult approximately .3 m apart. The adult began pecking grit about .2 cm in diameter and approached one of the offspring. As if it were being fed, the young bird gaped widely as the parent placed the grit in its mouth. The parent repeated this behavior until each fledgling had received approximately 4 pieces of grit. At this point one of the young birds started pecking grit.

I made a similar observation on 31 Aug. 1974 at the LaCrosse Municipal Airport. The observation distance was approximately 3 m, and it was clear that small pieces of gravel were being fed to the young birds. They did not, however, peck grit themselves This behavior might be an example of learning by prompting or imitation. Such imitative behavior is of obvious importance since the intake of grit is essential in seed eaters.—Doren Crook, *Biology Dept. Univ. of Wisconsin, LaCrosse 54601. Accepted 25 Feb. 1975.*

Predation by Common Ravens on feral Rock Doves.—About 100 Rock Doves (*Columbia livia*) have for many years inhabited Succor Creek Canyon, Malheur Co., Oregon. At least one pair of ravens (*Corvus corax*) inhabit the canyon. Over a 2-day period I saw ravens fly toward and dive at groups of doves sitting on projections along cliff faces. The doves were flushed by such maneuvers, but usually stayed close to the cliffs and were not pursued by the ravens. At 19:45 on 14 May 1975 one raven flushed a small group of doves from a ledge and one broke from the flock and flew 0.4 km across the canyon

closely pursued by both ravens. The dove landed on a small ledge near the base of the cliff under a narrow canopy of alder (*Alnus* sp.). Both ravens entered the trees above the dove and flushed it again. They forced the dove into the creek where it landed in an eddy along the shore. The ravens landed on the bank, one upstream and the other downstream of the dove; they chased it back and forth until one killed it with a sharp blow to the head. Without releasing its grip, the raven pulled the bird from the water and both ravens plucked and ate it.

I found several similar piles of dove feathers along the canyon walls and concluded that these piles represented predation by ravens.

On 20 May 1975 Sam Shaver and I flushed a pair of ravens from a freshly killed Chukar (*Alectoris graeca*) along Dry Creek, Malheur Co., Oregon. Evidence also suggested predation by ravens.

I am grateful to Jack Ward Thomas for improving this paper and to the Bureau of Land Management for financing my research.—Chris Maser, *Puget Sound Museum of Natural History, Tacoma, WA 98416*; Present address: *Range and Wildlife Habitat Laboratory, Route 2, Box 2315, La Grande, OR 97850.* *Accepted 5 Sept. 1975. Page costs paid.*

Hoarding of corn by Golden-fronted Woodpeckers.—During the periods 17–18 November and 14–17 December 1973, we observed Golden-fronted Woodpeckers (*Centurus aurifrons*) feeding on corn (*Zea mays*) at a Turkey (*Meleagris gallopavo*) feeding station. Shelled corn was exposed on a wooden platform (5 × 15 × 46 cm) in a wooded area 16 km E of Fort McCavett, Menard Co., Texas.

Each woodpecker would fly down to the feeder, seize a kernel of corn in its bill, fly to nearby dead live oaks (*Quercus virginiana*) and place the kernels under the bark in cracks or in other small openings. One bird worked at this operation for approximately 3 hours each day, carrying off and hoarding 30–50 corn kernels each 3-hour period. On 15 and 16 December, air temperature dropped to –10° C and never rose above 7° C. During this time woodpeckers ate about every fifth kernel by holding it with one foot and breaking the kernel into 3 or 4 manageable pieces. During both periods the woodpeckers drove Cedar Waxwings (*Bombycilla cedrorum*) and Cardinals (*Cardinalis cardinalis*) away from the corn.

There are reports of fruit and nut eating by Golden-fronted Woodpeckers (e.g., Leck, Wilson Bull. 81:264–269, 1969). We believe ours are the first observations of grain eating by this species, and there are no records to date of hoarding by them. Exclusion of other birds from the feeding station is consistent with behavior reported by Leck (op. cit.).—James W. Martin and James C. Kroll, *School of Forestry, Stephen F. Austin State Univ., Nacogdoches, TX 75961.* *Accepted 25 July 1975. Page costs paid.*

Biting in the Triumph Display of the Canada Goose.—The Triumph ceremony is a characteristic behavior pattern in the social life of all species of true geese. It is exclusively performed between birds which know each other and often occurs as a "greeting ceremony" when partners meet after a time of separation. It is also frequently observed during the period of territorial fighting in spring, both before and after attacks on other geese.

The first part of the ceremony, rolling (Fischer, Z. Tierpsychol. 22:247–304, 1965), is characterized by a loud "honking" vocalization in the Canada Goose (*Branta canadensis*). The neck is extended forward at an angle of about 45° to the ground and is waved up and down. The second part, cackling, is accompanied by a "snoring" sound. The head and neck are protruded almost horizontally to the ground. In this position the male may perform a thrust with his head, often terminated with a bite, toward the female who then immediately withdraws her head from the cackling posture and turns it to the side, or she may turn her head away from the male without first withdrawing the neck.

During the course of a study of the sequential patterning and the interactions between male and female in the ceremony I made some observations which may give a clue on the factors underlying the performance of the bite from the male.

Eight pairs of Canada geese were studied during the springs of 1973 and 1974 and about 300 hours of observation were recorded. More detailed descriptions of the ceremony and related behavior in the Canada Goose are given by Collias and Jahn (Auk 76:478–509, 1959), Raveling (Behaviour 37:291–319, 1970) and Radesäter (Ornis Scand. 5:87–101. 1974).

In Table 1 the number of male cacklings with a bite and the number of male cacklings without a bite are compared with respect to the orientation of the female to the male. Significantly more bites were delivered when the birds were meeting frontally than when they adopted more laterally oriented positions ($\chi^2 = 10.05$, df $= 3$, $p < 0.05$). A result similar to this was also obtained in an analysis of ceremonies eliciting fighting in juvenile geese (Radesäter, Behaviour 50:1–15, 1974).

The Triumph Display is regularly elicited when strange geese are coming too close to the pair in the territory. However, male biting in the ceremony seemed to be more likely in some situations than in others, obviously depending on the relative rank of the intruder pair. This difference was not due to any difference in the orientation between the partners during ceremonies elicited by intruders of higher or lower rank respectively.

If the intruder pair was superior in rank to the pair under observation, the male

TABLE 1

NUMBER OF MALE CACKLINGS WITH A BITE COMPARED WITH THE NUMBER OF MALE CACKLINGS WITHOUT A BITE IN TRIUMPH CEREMONIES WITH DIFFERENT ANGLES BETWEEN MALE AND FEMALE

	Angle			
	0–45°	45°–90°	90°–135°	135°–180°
Cacklings with bite	6	9	21	17
Cacklings without bite	50	30	40	38

was less likely to attack but his cacklings more frequently involved a bite (15 with a bite, 15 without) than was the case if the intruder birds were subordinate to him (2 with a bite, 17 without). This difference also holds true statistically ($\chi^2 = 6.35$, $df = 1$, $p < 0.01$). The male was also more likely to attack a subordinate pair (14 attacks out of 19 intrusions by subordinate pairs, 12 attacks out of 30 intrusions by superior pairs, $\chi^2 = 4.03$, $df = 1$, $p < 0.05$).

The occurrence of male nape biting or nibbling during the Triumph Display was first mentioned by Klopman (Mag. Ducks and Geese 12:6–9, 1961) who made the suggestion that sexual tendencies, revealed by its close resemblance to the bite performed by the male during copulation, might contribute to its occurrence. In a study of the associations between the Triumph ceremony and other behavior patterns, however, I could find no evidence that sexual tendencies were involved in the ceremony (Radesäter, Ornis Scand. 5:87–101, 1974). This study instead indicates that the Triumph ceremony is more closely related to agonistic behavior than to other behavior patterns. Ontogenetic data also suggest that aggressive tendencies underlie biting. In small goslings frontal meeting during cackling frequently turns into biting and fighting among the siblings. During these periods a marked rank order develops which is then regularly demonstrated in each cackling by the subordinate individual's facing away from the dominant bird (Radesäter, Behaviour 50:1–15, 1974).

In adult birds the biting seems to be correlated both with the releasing situation and with the season. Biting is much more frequently observed during the territorial period than during other seasons. Male biting is correlated with the rank of the intruder bird. In the case when the intruder birds are of superior rank the evoked aggression of the male is possibly inhibited from an "outlet" (as is demonstrated by the low number of actual attacks) but in this situation he is more apt to deliver a bite toward his own female. In this situation male biting fulfills the criteria of a "redirected activity" and indeed indicates that aggressive tendencies may effect its occurrence.

Although observational data are still fragmentary and more convincing results not yet available, one may speculate that one function of the Triumph Display in the Canada Goose is to allow the expression of activated aggressive tendencies in a peaceful way when such tendencies are inhibited from a natural outlet. It does not seem improbable that a ritualized male bite and a female appeasing signal might serve this function. It would also be possible that aggressive tendencies activated by the mere presence of the female in the territory might be canceled in this way in situations where it is prevented from an outlet, e.g. by an attack toward other geese.

The cackling of the Canada Goose thus can be said to involve a demonstration of rank between the partners. The performance of such dominance—subordinance rituals in meeting situations is also known for other species (Nelson, XVth Proc. Int. Ornithol. Congr. 1970:371–388) and it has been suggested that they may function to suppress aggression and thus allow a friendly meeting between presumptively hostile partners.

The influence of aggressive tendencies on the male bite and female facing away indicated that these factors might have influenced the development of the Triumph ceremony in geese.

This work was supported by a grant from the Swedish Natural Science Research Council (given to Prof. E. Fabricius), from the University of Stockholm and from the Helge Ax:son Johnsons Stiftelse.—T. Radesäter, *Division of Ethology, Dept. of Zoology, Univ. of Stockholm, Box 6801, S-113 86 Stockholm, Sweden.* *Accepted 13 Jan. 1975.*

Robin gathering nest material in October.—On 10 October 1974 I saw an American Robin (*Turdus migratorius*) gathering pieces of dried grass in Central Park, New York, N.Y. It was at 08:30, the temperature was 11° C, and many robins were singing. The bird was in a small grassy patch on a rock knoll. It held about 8 pieces of 5 cm long grass in its bill and continued to explore the area, picking up a few more pieces of grass, until it was chased away by another robin flying by. The first robin did not drop the grasses when it took off, but I could not see if it did so in flight before both birds disappeared from view. No robin returned to the site.

The age and sex of the robin gathering nest material could not be determined, but it had none of the spotting of the juvenal plumage, nor the noticeably darker head which some males have in fall. The robin which chased it was in similar plumage. I saw no signs of molt. Bent (U.S. Natl. Mus. Bull. 196, 1949) notes that the nest is built almost exclusively by the female, and that short pieces of grass are usually used by robins in the center of the nest, at the last stages of construction.

In searching the area during the next few days, I found no signs of a nest under construction, nor did I see any robin gathering nest material.

I have found one other record of a robin gathering nest material out-of-season, but not actually nesting. Brackbill (Wilson Bull. 85:238, 1973) saw a robin partially in juvenal plumage picking up and dropping pieces of fine dead grass on 22 August 1972.

Selander and Nicholson (Condor 64:81–91, 1962), in reviewing occurrences of fall nesting in North American birds, noted that many species resident in temperate latitudes have a brief period of sexual activity in the fall. This is associated with the partial recrudescence of the gonads from the preparatory or regenerative phase. In the American Robin, this period is evidenced by the singing heard in September and, most frequently, October (Howell, Am. Midl. Nat. 28:529–603, 1942). However, no records exist of other signs of breeding behavior in the robin at this season. In part, this may be due to the nature of robin courtship; even in spring, courtship and pair formation are inconspicuous, and there are no copulatory displays (Young, Am. Midl. Nat. 53:329–352, 1955).

Many of the recorded cases of out-of-season nesting in the genus *Turdus* may have been induced by unusual environmental stimuli, such as a prolonged period of mild weather, and perhaps confounding stimuli such as artificial light. Berger (Auk 63:668, 1966) found a robin incubating 3 eggs in January in Pennsylvania and Kress (Wilson Bull. 79:245–246, 1967) noted a robin which began a nest in Ohio in December 1965 from which 3 chicks hatched the next month. He suggested that breeding behavior may have been induced by stimulation of the gonads from the red light rays coming from colored lights on an enormous Christmas display across the street from the nest.

Several records exist for other members of the genus. Grummt (Vogelwarte 21:295–296, 1962) found a pair of Blackbirds (*T. merula*) which built a nest in the middle of a neon light in Berlin in December 1959. Young fledged the following February. Snow (Br. Birds 48:120–126, 1955) reports several nestings of the Blackbird and Song Thrush (*T. ericetorum*) during the very mild winter of 1953–54, but none of these nests were begun before mid-November. The only other October occurrence of nesting behavior I have found is Craster's (Br. Birds 50:77, 1957) report of a Song Thrush with a nest of 4 eggs on 11 October 1956. The nest was deserted by 18 October.

I thank Robert W. Dickerman and Helen Hays for suggesting sources and reviewing this paper.—Roger F. Pasquier, *235 East 73rd Street, New York, N.Y. 10021.* *Accepted 20 Jan. 1975.*

The Mexican chicken bug as a source of raptor mortality.—From 8 May to 3 July 1974, I examined the reproductive success of cliff-nesting raptors in northeastern New Mexico. The birds were nesting in extensive canyonlands made up of 6–35 m sandstone cliffs. Species observed included the American Kestrel (*Falco sparverius*), Red-tailed Hawk (*Buteo jamaicensis*), Prairie Falcon (*Falco mexicanus*), and Golden Eagle (*Aquila chrysaetos*). I found 32 cliff nest sites and 92 eggs and/or young.

The abandonment of one clutch of 3 Prairie Falcon eggs and death of 7 young Prairie Falcons (broods of 4 and 3) and a brood of 2 young Red-tailed Hawks I attribute to the presence of the Mexican chicken bug (*Haemotosiphon inodorus*) (Usinger, Monograph of Cimicidae, Horn-Shafer Co., Baltimore, 1966). These bugs feed by sucking blood from their hosts. I counted as many as 30 bugs attached near the eyes and at the base of legs and wings of a single week-old Prairie Falcon. Usinger (1966:475) identified the Mexican chicken bug's native hosts as birds of prey. It has been found in the nests of the California Condor (*Gymnogyps californianus*), Golden Eagle, Great Horned Owl (*Bubo virginianus*), and Barn Owl (*Tyto alba*) (Hicks, Checklist and Bibliography on the Occurrence of Insects in Bird Nests, Iowa State Coll. Press, Ames, 1959; Hicks, Iowa State J. Sci. 36:233–344, 1962).

The Mexican chicken bug commonly infests poultry; Usinger (1966:261) suggests that predatory birds could become infested with the bugs by preying on chickens. This seems unlikely at the nests I observed, since I visited most ranches in the area and found chickens at only one location. In addition, I inventoried remains of 65 prey items and examined 87 pellets and found no evidence of chickens having been consumed.

H. inodorus is indifferent to light (Lee, Pan-Pac. Entomol. 30:159–160, 1954) and can be active throughout the daylight hours. Population densities can reach very high levels; Lee (Pan-Pac. Entomol. 31:47–61, 1955) reported 1778 bugs in a single Barn Owl nest.

My thanks to J. Langford and P. A. Platt for their valuable assistance in the field; to Dr. J. C. Lewis, Dr. G. M. Sutton, and Dr. J. S. Barclay for their encouragement; to the Scientific Research Society of North America, The Society of Sigma Xi, and OSU Research Foundation for financial assistance; and to Dr. D. E. Howell for confirming the identification of *H. inodorus*.—Stephen W. Platt, *Dept. of Biological Sciences, Oklahoma State Univ., Stillwater 74074.* *Accepted 31 Jan. 1975.*

American Kestrels sit on Wood Duck eggs.—While conducting a study of breeding Wood Ducks (*Aix sponsa*) in nest boxes at Great Swamp National Wildlife Refuge, Morris Co., New Jersey, I found 2 female American Kestrels (*Falco sparverius*) that were sitting on Wood Duck eggs as well as their own.

The first such occurrence, initially noted on 17 April 1973 involved incubation of 5 kestrel eggs and 1 duck egg. This box, when checked on 27 March, contained only pine shavings. On 17 April it contained several unidentified down feathers as well as 2 pieces of fur. The viable duck egg was found among kestrel eggs. The shavings formed a cup

similar to that found by Richards (Condor 72:476, 1970) so that the duck egg remained with those of the kestrel without any attention required on the part of the kestrel. I numbered all eggs with pencil.

On 3 May the bird was incubating 4 kestrel eggs and the same duck egg. The pencil markings had been rubbed off somewhat, presumably due to the incubating bird. There was no trace of the fifth kestrel egg. The positions of all remaining kestrel eggs had been changed so that each egg had been moved at least 90 degrees. The duck egg, however, had been moved only about 45 degrees. It now was situated on the outside of the clutch, but it still remained with the kestrel eggs in the cup of shavings without rolling out.

Apparently the kestrel eggs were near their hatching date because my next inspection on 24 May revealed 3 young kestrels with well-developed plumage including brownish-red primaries and rectrices. Many regurgitated pellets were present but the Wood Duck egg was gone.

The other instance of kestrel occupation occurred in a Wood Duck box with 2 compartments. During an inspection on 24 April I was repeatedly harassed by a flying kestrel (sex unknown) while observing a kestrel egg in one compartment. The kestrel was sitting in the compartment on 8 May. It continued to sit on the egg throughout my inspection and note-taking. In the adjoining compartment, I found 33 Wood Duck eggs abandoned and removed them to allow renesting by other ducks. The kestrel sat on at least one duck egg, again atop a 10 cm pile of shavings. Since the bird was sitting on the clutch, the positions of any other eggs were not noted. The duck egg, however, was located partly beneath the bird's right shoulder. Approximately half of the egg's surface was exposed. I do not know if the shavings formed a cup.

On 20 June I found one young kestrel about 3 weeks of age in the box along with regurgitated pellets and 2 duck eggs. One of the duck eggs was still viable. The other kestrel egg was missing. The young kestrel was gone by 2 July.

A similar report, published by Bent (U.S. Natl. Mus., Bull. 170, 1938), involved a kestrel sitting on an egg of a Common Golden-eye (*Bucephala clangula*).—Stephen J. Zipko, *Dept. of Zoology, Rutgers Univ., Newark, NJ 07102.* *Accepted 30 Jan. 1975.*

Wildlife occupying potential Wood Duck tree nest sites.—Natural cavities suitable as Wood Duck (*Aix sponsa*) nest sites are often judged scarce and normal management is to erect nest boxes to alleviate the shortage. This procedure is often quite effective (McLaughlin and Grice, Trans. North Am. Wildl. Conf. 17:242–259, 1952; Bellrose et al., J. Wildl. Manage. 28:661–676, 1964). Wildlife other than Wood Ducks often use the nest boxes and natural cavities so that many are unavailable for Wood Duck use. Several investigators have listed nest box occupants (Brown and Bellrose, J. Wildl. Manage. 7:298–306, 1943; Frank, J. Wildl. Manage. 12:128–136, 1948; McLauhglin and Grice, op. cit.; Klein, N.Y. Fish & Game J. 2:68–83, 1955), but few have studied the occupants of natural Wood Duck nest sites (Bellrose et al., op. cit.; Wier, Wood Duck Manage. and Res. Symp. p 91–112, Wildl. Manage. Inst., Wash. D.C., 1964). This note summarizes data on this subject which were gathered during a Wood Duck production habitat inventory (Boyer, M.S. thesis, Central Michigan Univ., 1974).

The area of study was the Shiawassee National Wildlife Refuge in east-central Michigan. Within the Refuge, the Tittabawassee, Cass, Shiawassee, and Flint rivers, plus several smaller creeks converge to form the headwaters of the Saginaw River. The Saginaw Valley is characteristically flat and is subject to extensive spring flooding. The

Table 1
Wildlife Using Potential Wood Duck Nest Sites in Natural Cavities and Nest Boxes on Shiawassee National Wildlife Refuge in 1972 and 1973

Species	Cavities		Boxes		Total	
	No.	%	No.	%	No.	%
Wood Duck (*Aix sponsa*)	4	5	6	11	10	7
Hooded Merganser (*Lophodytes cucullatus*)	1	1	0	0	1	1
Downy Woodpecker (*Dendrocopos pubescens*)	1	1	0	0	1	1
Tree Swallow (*Iridoprocne bicolor*)	0	0	3	5	3	2
Starling (*Sturnus vulgaris*)	2	2	4	8	6	3
Red-winged Blackbird (*Agelaius phoeniceus*)	0	0	1	2	1	1
Raccoon (*Procyon lotor*)	12	13	1	2	13	9
Squirrel (*Sciurus niger* or *Tamiasciurus hudsonicus*)	14	16	0	0	14	10
Deer mouse (*Peromyscus* sp.)	0	0	1	2	1	1
Bees (*Apis* spp.)	0	0	3	5	3	2
Unoccupied	52	62	35	65	91	63
Total	90	100	54	100	144	100

Refuge's 19,500 ha included 39% forest, 44% croplands, and 15% marsh and open water. Red maple (*Acer rubrum*), eastern cottonwood (*Populus deltoides*), green ash (*Fraxinus pennsylvanicus*), and bitternut hickory (*Carya cordiformis*) were the most abundant trees.

I searched forest stands for trees with openings of 8 cm or greater. These were subsequently climbed and cavity dimensions, inside and outside, were recorded so that each cavity could be rated as to its value as a potential Wood Duck nest site. Fifty-five nest boxes were also checked for use. Animal sign in, outside, and near the cavity or box was used to determine use. A summary of wildlife using the potential natural nest sites and boxes is presented in Table 1.

Forest evaluation data showed that 48.1% of all trees on the Refuge were red maple. Cottonwood, green ash, and bitternut hickory made up 9.9%, 9.2%, and 6.0%, respectively. Suitable nest sites were found predominantly in red maples (62 of the 90 located). The remaining 28 sites were scattered among 8 species. Most of the natural nest sites (65%) and boxes (62%) were unoccupied, suggesting that competition for potential Wood Duck nest sites was low. All nest sites were close (1.6 km or less) to adequate Wood Duck brood rearing habitat, so that all sites were available for use by Wood Ducks.

I would like to acknowledge the helpful and thoughtful guidance of Dr. John N. Krull throughout the original period of field work. Thanks are also due Mr. Robert E. Timmerman, Refuge Manager. The present paper was partially supported by Commonwealth Associates Inc.—Roger L. Boyer, *Biology Dept., Central Michigan Univ., Mt. Pleasant 48858. (Present address: Landplan Systems, Commonwealth Associates Inc., 209 E. Washington Ave., Jackson, MI 49201.)* *Accepted 3 Feb. 1975.*

ORNITHOLOGICAL NEWS

At the 93rd Stated Meeting of the American Ornithologists' Union held in Winnipeg, Manitoba, August 25–29, 1975 the following officers were elected: President, John T. Emlen; First Vice-President, Wesley E. Lanyon; Second Vice-President, Kenneth C. Parkes; Secretary, George E. Watson; Treasurer, John A. Wiens.

Alexander Wetmore was elected Honorary President.

The Brewster medal for meritorious work on birds of the Western Hemisphere was awarded to Jürgen Haffer. The Coues Awards for contributions that have had important impacts on the study of birds within the Western Hemisphere were given to Walter Bock, Richard F. Johnston, and Robert K. Selander.

Bernard Rensch of Germany was elected as an Honorary Fellow and Phillip A. Clancy (South Africa), Kai Curry-Lindahl (Sweden), Eberhard Gwinner (Germany), Colin Pennycuick (United Kingdom), and William H. Phelps, Jr. (Venezuela) were elected Corresponding Fellows.

In 1976, the American Ornithologists' Union will hold its annual meeting at Haverford College, Haverford, Pennsylvania, August 9–13.

EBBA Research Grant

The Eastern Bird-Banding Association is offering again a research grant of $250 to an undergraduate or graduate student in ornithology who is using bird banding as part of the project. The applicant must be attending a college or university within the United States. Applications (in triplicate) and other supporting evidence should be sent before 1 March 1976 to the Chairman of the Memorial Grant Committee: Bertram G. Murray, Jr., Dept. of Science, Rutgers Univ., New Brunswick, NJ 08903.

Louis Agassiz Fuertes and Margaret Morse Nice Awards

Fuertes Awards are devoted to the encouragement and stimulation of young ornithologists. One particular desire is the development of research interests among amateur ornithologists and students. Any kind of ornithological research may be aided. Recipients of grants need not be associated with academic institutions. Each proposal is considered primarily on the basis of possible contribution to ornithological knowledge. Although grantees are not required to publish their studies in *The Wilson Bulletin*, it is hoped that they will submit their manuscripts to the editor of *The Wilson Bulletin* for consideration.

Most of the statements applicable to the Fuertes Awards are also applicable to the Nice Award. However, the Nice Award is limited to applicants not associated with a college or university. It is intended to encourage the independent researcher without access to funds and facilities generally available at the colleges. High school students are eligible.

In some years 2 Fuertes Awards have been made, in some years, one. Amounts have been between $100 and $200. One Nice Award is made annually, in the amount of $100.

Interested persons may write to Stephen M. Russell, Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, Arizona 85721. Completed applications must be received by 15 April 1976. Final decisions will be made by the Council at the annual meeting of the Society, 3–6 June 1976.

Frank M. Chapman Fund

The Frank M. Chapman Fund gives grants-in-aid for ornithological research and also post-doctoral fellowships. Applications are due on 15 February and 15 September. In-

formation on form and content of applications may be obtained from the Frank M. Chapman Memorial Fund Committee, The American Museum of Natural History, Central Park West at 79th St., New York, N.Y. 10024.

Peregrine Falcon Bibliography

The U.S. Fish and Wildlife Service is compiling a bibliography with abstracts of English language literature, both books and periodicals, on the Peregrine Falcon (*Falco peregrinus*). Authors who wish to have their articles included in this work should send two reprints, copies, or abstracts to: Dr. Richard D. Porter, I.F. & R.E.S. Shrub Lab, 735 North 500 East, Provo, UT 84601.

Articles in which the Peregrine Falcon is mentioned but is not the main subject, and articles in foreign languages with English summaries are also wanted.

Request for Assistance

Color-marked birds of prey.—Research personnel at the Snake River Birds of Prey Natural Area would like your help in recording birds-of-prey movements. They have placed color-coded vinyl wing markers and/or yellow "paint" on juvenile birds to help determine post-fledging movements. Wing markers and tail paint may show only on the dorsal surface of the birds. Ninety-three birds (Golden Eagles, Prairie Falcons, Red-tailed Hawks, and Ravens) were marked this year and the program will continue until 1980. If birds so-marked are observed, please note the following information: 1, species of bird and how marked; 2, location of sighting (state, county, distance from nearest landmark); 3, date of sighting; 4, observer's name and address; and 5, activity and condition of the bird. Please send this information to: Dean Bibles, District Manager, Boise District, Attn: Mike Kochert, Bureau of Land Management, 230 Collins Road, Boise, ID 83702.

International Commission on Zoological Nomenclature Announcement—A.N. (s.) 97

Required six months' notice is given of the possible use of plenary powers by the International Commission on Zoological Nomenclature in connection with the following name listed by case number: (see Bull. Zool. Nom. 32, part 3, 22nd September, 1975).

2108. *Thamnophilus ruficollis* Spix, 1825 (Aves, Formicariidae): proposed suppression.

Comments should be sent in duplicate, citing case number, to the Secretary, International Commission on Zoological Nomenclature, c/o British Museum (Natural History), Cromwell Road, London, S.W.7 5BD, England. Those received early enough will be published in the Bulletin of Zoological Nomenclature.

A Word to Members

The Wilson Bulletin is not as large as we want it to be. It will become larger as funds for publication increase. The Society loses money, and the size of the *Bulletin* is cut down accordingly, each time a member fails to pay dues and is put on the "suspended list." Postage is used in notifying the printer of this suspension. More postage is used in notifying the member and urging him to pay his dues. When he does finally pay he must be reinstated in the mailing list and there is a printer's charge for this service. The *Bulletin* will become larger if members will make a point of paying their dues promptly.

ORNITHOLOGICAL LITERATURE

Avian Energetics. By Raymond A. Paynter, Jr. (ed.). Publications of the Nuttall Ornithological Club. No. 15. Cambridge, Mass. 1974: viii + 334 pp., 57 figs., 48 tables, 1 appendix. $17.00. (Obtainable from the Nuttall Ornithological Club, c/o Museum of Comparative Zoology, Harvard Univ., Cambridge, MA 02138.)—Many ecologists are oriented toward understanding the complex environmental-organism interactions that underlie the adaptive properties of organisms. Recent reviews of the "strategies" with which organisms increase their inclusive fitness have explored how organisms might partition their time and energy in some "optimum" manner. A basic assumption is that constraints on time and energy expenditures are important determinants of the evolutionary success of a genotype. When measurement of benefits and costs is in the same units, energy or time, the potentially measurable selective forces acting on a single adaptive trait range effectively across all biologic attributes. For example, as Robert Ricklefs discusses in this volume, the question of growth rates of young birds is related to an interconnected series of factors such as food quality, foraging efficiency of the adults, predation pressure on both adults and young, the probability that the parents would do better by abandoning the present brood and trying to raise another brood later, the difficulty that the young face in finding food, and so on. These complex interactions at least theoretically become tractable when viewed in the units of the common currency, energy. The common thread through all these papers is that energetics is probably an important key to understanding ecological organization at whatever level of interest.

Fortunately for avian ecologists, comparative physiologists have refined the methods (and the actual estimates) of estimating energy expenditures of organisms. Most of this work has been principally in the laboratory and there is a growing awareness, expressed by the authors in this volume, of the need for additional refinements of the laboratory techniques for use in natural situations. The paper by James King provides a summary of available techniques of field estimates of energy expenditures and indicates their strengths and weaknesses.

As King emphasizes, the possible views that can be taken of the problem of field measurement of energy expenditures are as broad as the questions being asked by the field ecologist. Although the authors, principal discussants, and audience at the original symposium disagreed somewhat over the required detail of measurements, techniques are now available to ask questions of individual organisms in a microenvironment. William Calder's detailed analysis of the microenvironment of a nesting hummingbird verifies the importance of such a detailed approach to well-phrased questions. However, as Eugene Odum reiterates with his analogy between a microscope and a "macroscope," not all questions about energetic expenditures can be approached fruitfully at this extremely detailed level; there is a necessary compromise between specificity and generality in any biological investigation. Calder has provided nearly the complete range with his discussion of the relationships among physiological and anatomical variables related to energetics and body weight of birds. His approach to the generality of certain adaptive traits in birds, presumably limited evolutionarily by energetic constraints, provides simple predictive equations, usually logarithmic, that relate each variable to body weight, independent of species. Calder emphasizes that his equations, which bring together a diverse literature, provide a starting point for understanding species which deviate from the expected relation. The use of these equations as initial hypotheses should spur work in many areas of avian energetics.

King also generates predictive equations for total energy budgets of birds on a seasonal and daily basis. More than general statements about what ought to be happening are difficult with so few seasonal data available, a clear signal to future ornithologists of an important area of research. King is on slightly firmer empirical ground with daily energy expenditures and provides comparisons among some birds and rodents. He ends with a discussion of the data that he thinks would provide a firmer empirical base for models of the interactions of organisms with their microenvironment and with each other.

Some problems inherent in the energetic approach to understanding ecological organization and adaptive strategies are brought out forcefully by Robert Ricklefs in his first rate review of the energetic requirements of reproduction. Ricklefs is not concerned with some major aspects of energy use in reproduction, such as the mating system, pair formation, nestbuilding, and other behavioral steps leading to the actual production and growth of the young. He rather discusses the costs of the production of functional reproductive organs and eggs, incubation, and growth of the young. At each step he provides clear summaries of much of the available literature and makes detailed comparisons between distinct adaptive types, e.g., growth rates of precocial and altricial young. His essay ends with an attempt to integrate energy expenditures into the complex of adaptations by which a genotype enhances its prospects of being represented in future generations.

Each of the first 3 authors draws on physiological measurements from the laboratory and field to estimate energy expenditures. Flight, the mode of energy expenditure nearly unique to birds among vertebrates, has also been one of the most difficult to measure. The last paper in this volume, by Vance Tucker, returns to the theme of coupling laboratory and field data in assessing energetic costs of free-living birds. His essay also illustrates the importance and frustration associated with the microview of energy expenditures—importance because his theoretical calculations and wind tunnel experiments have identified important variables in flight costs, and frustration because of the many variables that must be accurately measured in a free-living bird to precisely estimate flight costs. However, Tucker provides estimates of the impact of these variables on flight cost, leaving each investigator to decide if it is essential to measure particular variables. The advances made by Tucker and C. J. Pennycuick in England in the last few years in our understanding of flight energetics are a tribute to their perceptivity and ingenuity in treating a difficult problem. They have drawn heavily from aeronautical engineering theory and find remarkably close relations between theory and data. The importance of their work to an understanding of energetic organization of ecological systems will be obvious from the number of future citations of their work.

The rapidly expanding field of avian energetics depends heavily on the earlier work of avian physiologists and ecologists, 3 of whom were principal discussants at the symposium and whose comments have been printed in full (and expanded in the case of Charles Kendeigh) following each paper. The organizer of the symposium, William Dawson, is to be congratulated on his choice of participants. He also was responsible for the extremely helpful appendix of conversion constants for the international system of units used in avian energetics.

This volume is mostly concerned with only one half of the energy equation, the expenditure of energy. Although each author was cognizant of the problem, there is almost no discussion of energy intake, especially in free-living birds, principally due to a lack of field techniques for measuring energy intake. The intake half of the energy equation will have important ramifications on how energy and time are spent by an

organism, primarily through determining how much time and energy must be allotted to maintaining energy income, and thus effectively limiting the available time and energy for other expenditures. A further difficulty, mentioned by several contributors, is the lack of information on the role of nutrient intake in determining ecological organization. In this respect the plant ecologists are far ahead of animal ecologists. However, these deficiencies point out the relative infancy and bright future of the field of avian energetics.

The speed of development of this field speaks well for the foresight of the Nuttall Ornithological Club, sponsors of the symposium, in identifying a field of ornithological inquiry that would be an important, emerging field in the 1970's. The goal of the club to lead ornithology into the 70's rather than reminisce about the past is achieved admirably with the present volume. In an emerging field it is important that results of such a symposium appear in print as soon as possible. The editor is to be congratulated for limiting publication time to about one year following the symposium, and in a volume that is remarkably free of printing errors.

To modify slightly a statement by George Bartholomew, one of the discussants, this volume will be an essential reference for all workers in the field of avian energetics and will provide important summaries for the full spectrum of biologists.—Larry L. Wolf.

The Life of Birds, 2 vols. By Jean Dorst. Translated by I. C. J. Galbraith. Columbia Univ. Press, N.Y., 1974: 718 pp., 110 text figs., 32 black-and-white photos. $35.00.—Publication of these volumes, authored by a well-known ornithologist and produced by a prestigious press, is calculated to rouse anticipation. Even the price, although one to blanche at, would seem to indicate excellence. Intentions voiced in the Introduction set an interesting stage: to concentrate "on the adaptations birds have made to the various environments they have colonized" and to produce an "essay on the ecology of birds . . . not so much for the specialist as for the well-informed public."

Reviewers, by tradition, are concerned with how well the author has fulfilled his intention. Having finished 689 pages of text, however, this reviewer regards it inappropriate to address himself entirely to this charge. More pertinent, it appears, is an evaluation of the finished "product" the press has presented the public, a public, incidentally, which has come to expect outstanding publications in biology from Columbia's press.

It has been customary to employ proofreaders to eliminate mechanical errors in manuscript proofs. Is it possible that the bibliography after each chapter was not proofread? The first chapter of Volume 2 (Chapter 19) contains 4 references which are not in the bibliography. From the next chapter one reference has been omitted and, although "Davidson (1968)" is cited twice in Chapter 21, this reference was left out. No fewer than 5 references have been omitted from the bibliography of Chapter 23. Other chapters have suffered similar careless compilation of bibliographic citations. To "well-informed" readers a bibliography has some importance.

The proofreading—or lack of it—merits further comment. How is it possible that no one entrusted with the manuscript's proof discovered that Chapter 27 is followed by Chapter 29 and the latter by 28! A column of a table (p 142) is empty of any figures. The captions for plates 8 and 9 are apparently reversed. An ornithologist would have hastened to asterisk the Pelecanoididae (p 352) to signify that this taxon is also exclusively marine. And, couldn't *someone* have corrected "*Anus*" (p 514) to *Anas*! Such editorial *faux pas* well emphasize the careless handling this manuscript has had.

Having paid the price of these volumes, the buyer might well, on inspecting the

illustrations, wonder if in some way a dreary joke was not being perpetrated on him. Figure 2 looks as though it might have been inspired by works of Volcher Coiter or Pierre Belon. To me such text figures as Nos. 3, 4, 17, 18, 19, 27, 30, and 33 are largely meaningless. Many of them are indistinctly reproduced (e.g., 3 and 4) and many need labels (e.g., how can anyone interpret the lower drawing of Fig. 33?). Finally, what of the 32 black-and-white photographs which are, it would seem, intended as "dessert and coffee" of the text? Most of these are mediocre examples of the art of photography. Many are too dark (e.g., 10a, 31, 32), some are out of strict focus (10b, 15), some are confusing (17), and few have merit with respect to composition.

It is a pity that the French edition could not have been carefully translated. The English prose is not crisp, it is exasperatingly prolix, overwhelmingly dull, sometimes downright confusing, and altogether too often ungrammatical. I have selected some examples. "Although certain forest species do occupy the guinean [*sic*] savannas these do not include any whose ecological needs restrict them to the dense forest"—(p 508). "Quite possibly most Polynesian islands are too small to give rise to such evolution, which are known to be produced only under precise geographical conditions"—(p 559). "These incomparably aerial vertebrates have exploited this mobility to make themselves dominant in the highest layers of vegetation and all other niches which demand it to the full"—(p 576). "The principal characteristics of migration is its perfect regularity" —(p 616).

I suspect that many of the unusual terms and statements one stumbles over throughout the text are errors of translation and not those of Dorst. I cannot believe that Dorst would assign (p 69) herons and egrets along with ibises and spoonbills to the same family, Ardeidae. I find it difficult to credit him with such statements as the following. "Birds have adapted to all diets and feed on everything on earth"—(p 62). "Apart from a few raptors which hunt other birds, all carnivorous birds live on insects and on vertebrates of other classes"—(p. 576). ". . . birds have adopted every possible diet and are established in all available niches"—(p. 574). Repeatedly it is stated (e.g., p 589) that "birds are closely dependent on the environment." How many animals aren't? Can Dorst have depicted (Fig. 98) the breeding range of the American Robin so incompletely? Careful refereeing by an ornithologist would have eliminated these and *many* other inaccuracies.

In addressing myself to the subject matter of the text, I can but admit to disappointment at much of Volume 1. The "well-informed public" might better turn to the several current texts of general ornithology for the information covered by this volume. These texts are written in a prose that is not awkward and they are not studded with inaccuracies. The reader should not be given such information as "there is no true muscle in these lower segments of the leg"—(referring on p 38 to the tarsometatarsus and the phalanges) or that (p 189) the many races of the Song Sparrow "are confined to the western coast of the United States."

In my opinion the 10 chapters of Volume 2 which deal with the avifauna of the major biomes of the world are the most useful part of the text. The discussions of deserts, tropical savannas, rainforests, etc. are interesting. It would have enhanced these chapters, however, if simple maps showing the extent of the biomes had been furnished. Pictures from these biomes would have added greatly to appreciation of them. What temperate zone resident, for example, can contemplate mangrove forests without some depiction of their morphology? Who is able to appreciate the distribution of these forests without a map?

"The touchstone of university press publishing continues to be high editorial merit, and no press has relaxed this standard in building its publishing program." So wrote the Executive Director of the American University Presses, Inc. in a letter to the *New York Times* (dated 17 April 1975). This letter was in response to comments by Alden Whitman (*New York Times*, 12 April 1975) regarding transformation of university presses into "profitable, best-seller ventures." Few would wish to deny university presses the advantages of "best-seller" books. But, in assuring themselves of such profit, presses may be tempted to economize to the extent of compromising careful refereeing, proofreading, adequate translating, and good illustration. In my opinion this has occurred in production of the "Life of Birds." It is to be hoped—fervently—that these volumes will not mark further departure from the ways of careful editing of scholarly manuscripts, ways which have been established over such a long and productive period of publication by Columbia and other outstanding university presses.—Oscar T. Owre.

Population Ecology of Migratory Birds. Bureau of Sport Fisheries and Wildlife, Wildlife Research Report 2, Washington, D.C., 1972: x + 278 pp., paperbound; no price given.—This collection of 11 papers stems from a symposium held at the Migratory Bird Populations Station, U.S. Bureau of Sport Fisheries and Wildlife, in 1969 to celebrate the dedication of the Ira N. Gabrielson Laboratory. Publication of the papers was delayed until 1972, and the report was not distributed until late 1973. Unfortunately, relatively few copies were printed, for the volume was out-of-print shortly after the initial distribution.

The papers included in the volume address migratory bird populations in a variety of ways. Some (Williamson, Eberhart, Geis, Henny and Wight) are chiefly concerned with ways of analyzing banding and census data to reveal aspects of population dynamics, while others (Carrick, Drury and Nisbet, von Haartmann, Dzubin and Gollop, Boyd) provide detailed descriptions of populations. One paper reviews migratory pathways of waterfowl (Bellrose), and a concluding summary paper by Hickey reviews the major points and their implications.

The stated objective of the symposium is to review the current status of our knowledge of migratory bird population dynamics, with special reference to the use of banding data in such studies. If this collection of papers is representative, we apparently know just enough about avian population dynamics to realize that good generalizations (and good data) are hard to come by. Carrick's paper, for example, summarizes in considerable detail his long-term studies of Australian magpies, Royal Penguins, and Silver Gulls, and provides a wealth of individual life history information. But despite the almost unparalleled intensity of his studies, good information on mortality factors is largely lacking. The paper by Drury and Nisbet details the population movements of New England Herring Gulls, and like Carrick's studies, indicates that natural populations are disturbingly complex in their dynamics. Their attempt to provide adaptive arguments for the observed patterns is only moderately successful (although intriguing). The contributions of Boyd and of Dzubin and Gollop encounter similar difficulties in discerning crisp cause-effect relations in waterfowl population dynamics. Collectively, these studies suggest that intelligent management of migratory bird populations may be much more difficult than is commonly conveyed in wildlife curricula, and that much of the theoretical framework of armchair population ecologists may be of only limited applicability to real world situations.

Like most symposium collations, this one is spotty in quality and stimulation level. The 4 papers noted above provide a wealth of detailed information about specific populations.

Other contributions deal more explicitly with methods of population analysis, at times in a superficial manner. Overall, the contributions are characterized by a general lack of recourse to statistics (with the exception of Eberhart's model) or to population or evolutionary theory (with the exceptions of Drury and Nisbet and Dzubin and Gollop). Genetic factors influencing population dynamics receive only fleeting (and rather fumbled) consideration.

This volume thus provides a rather mixed sampling of descriptive studies of populations and their analysis, but contributes little to the theoretical framework of population biology. Given the 4 year publication lag, it is perhaps just as well that "facts" rather than theory (which changes rapidly) were emphasized.

A final word must be said about the publication itself. It is bad enough that the volume was printed in insufficient quantity to make it generally available, but if my copy is any indication, those copies which were printed will not last long. Mine fell to pieces before I was halfway through it.—John A. Wiens

Breeding Biology of the Gray Gull, *Larus modestus*. By Thomas R. Howell, Braulio Araya, and William R. Millie. Univ. of California Publ. in Zoology, Vol. 104, Los Angeles, 1974: 54 pp, 21 plates, 7 figs.; paper cover. $2.50.—This volume describes the breeding behavior and ecology of the Gray Gull, a species heretofore never studied on the breeding grounds. As such, it is a much needed and welcomed study. I feel it is a major contribution to our understanding of gull biology and behavior, and I recommend it to ornithologists strongly.

The Gray Gull is an abundant species on the Pacific coast of South America, and breeds in the barren deserts of the interior. The monograph covers courtship and mating behavior, clutch and egg size, incubation behavior, chick behavior, and mortality factors. Courtship behavior is described on the coast as well as inland. Incubation behavior includes incubation temperatures and the length of the incubation period. The sections dealing with chicks discuss nestling care, growth rates, food, and thermoregulation. Other sections include predation and other mortality factors on the young.

The methods section seems brief and does not explain how data were collected. The dates of the field work were unclear. For example, p 8 states that Howell was there from 30 November–9 December 1968, and p 9 states that he left 15 December.

Early sections of the monograph describe habitat, courtship displays, and colony size. The description of courtship behavior is clear, useful, and allows for a comparison with Moynihan's work (1962: Behav. Suppl. 8) on Gray Gull displays away from a breeding colony. As these are the only descriptions of Gray Gull displays on the breeding grounds, they are an important and invaluable addition to the gull literature. A limit on time, no doubt, prevented quantification of these displays. For example, the frequency of displays, the position of displaying birds, and sonograms of vocalizations are not given. I wonder how difficult it was to sex birds for behavioral descriptions without collecting birds or sexing them from copulation.

The section on size of colony and distribution of nests shows that nest distribution was random within their one 100 × 100 m study site. They mention, however, that nests were not uniformly distributed throughout the 5.5 km^2 colony area. No analysis of edge versus interior nests was made (cf. Coulson, Nature 1968: 478–479).

The point is made early that the behavior and ecology of the Gray Gull must be adapted to the harsh desert environment. Much of the monograph deals with its adaptations to this habitat. I wish the data were better quantified. They state that at dawn the ambient temperature is "only a few degrees above 0°" and by "mid-morning solar heat becomes

intense". In the "early afternoon" "strong" WSW winds begin, and "lower" the surface temperature (p 18). A partial graph of ambient temperature is given on p 20, but a complete 24 h graph would have been useful. They collected data on temperatures on the substrate in the sun and shade, inside 1 egg, and at the surface of 1 shaded egg. The temperatures of both experimental eggs reached lethal levels of 44° C. Thus, incubation must begin with the laying of the first egg to prevent death of the embryo.

The sections on incubation period, chicks, and nestling care contain much information on the reproductive biology of the Gray Gull, and are valuable for comparative purposes. Chick mortality resulted from exposure or starvation. Only chicks over 100 g in weight were able to thermoregulate in still air.

The discussion section includes ethology, advantages and disadvantages of desert nesting, taxonomic relationships, plumage color, and origin of desert nesting. The nature of the data lend themselves to a discussion of adaptations to desert nesting (present) and a comparison with other desert adaptations in birds (not present). They comment on the non-predatory behavior of Gray Gulls toward their own eggs and chicks, saying it is a derived condition (p 46). I see no reason to conclude this, as a good many of the "primitive" gulls do not prey on their own eggs and chicks.

The plates are excellent, clear, and lend much to the behavioral descriptions. My copy is clean and clear. In general I found the monograph to be readable and a major contribution to our understanding of gull biology. It covers the scope of the breeding cycle, and is thus very useful for comparison with other gulls. I recommend it for biologists interested in gulls, life histories, behavior, breeding biology, temperature regulation, and desert adaptations.—Joanna Burger.

Waterfowl: Their Biology and Natural History. By Paul A. Johnsgard. University of Nebraska Press, Lincoln. 1968: 138 pp., 89 black-and-white and 59 col. photographs, 16 figs. Introduction by Peter Scott. $8.95.—In this single inexpensive text Johnsgard set out to provide nonprofessionals with a concise summary of the general biology of waterfowl and to provide photographs of all 142 living species of waterfowl of the world. Drawings of 4 species and 2 subspecies that are extinct are included. Laymen may be confused over some scientific and common names that Johnsgard uses. I agree with his use of scientific names even though they are not all recognized in the AOU Check-list. However in a text for nonprofessionals, the recognized names seem more appropriate.

Most photographs were taken by the author. Many color photos are excellent and provide good examples of adults in definitive alternate plumage (e.g. pl. 31. White-backed Duck and pl. 52. Comb Duck). As many as 13 of the black-and-white photos are of such poor quality that their use in the text is questionable (e.g. pl. 59, Cotton Pygmy Goose and pl. 83. Brown Pintail). This is unfortunate because Johnsgard is an accomplished photographer. Inclusion of the scientific name and range description near each photo would have been a valuable addition. Both are usually given in books for laymen.

Some of the figures are excellent. I especially like Fig. 1; however, laymen may not recognize these distinctive drawings of heads that represent the Tribes in the family Anatidae. In Fig. 3 restricted ranges might better be depicted by range maps rather than drawings of the species. In Chapter 4. Sound Production, syrinx variability (Fig. 5) is of interest to professionals, but I question the relevance of this figure for laymen. Nor are Figs. 6 (trachea of a Bewick's Swan) and 16 (Trumpeter Swan) of great enough importance to require an entire page.

The first 8 chapters provide information on distribution and migrations, ecology and general behavior, sound production, social behavior, breeding biology, molts and plumages,

and evolution and hybridization. In Chapter 9 Johnsgard discusses the scant information on extinct and near extinct species plus the taxonomic position of several perplexing species (e.g. Marbled Teal, Coscoroba Swan, White-backed Duck, and Freckled Duck). A discussion of endangered species is the primary theme in Chapter 10, Waterfowl, Man and the Future. Johnsgard might have been more emphatic about the decline of waterfowl numbers related to habitat loss because of human activities. This is a fact that all too few laymen realize.

My experience with students suggests that the use of the key in Chapter 11 would require drawings and possibly a good ornithological text or laboratory manual before the inexperienced person could use the key effectively. The annotated list of Anatidae in Chapter 12 is a helpful listing that is especially valuable to students.

I found the book inadequate for students taking a course in waterfowl biology and too filled with technical details for laymen. Even so, "Waterfowl" is a book that persons interested in waterfowl will want in their library. Considering the cost of other works on waterfowl of the world, $8.95 is a bargain.—Leigh H. Fredrickson.

The Avifauna of the Kakamega Forest, Western Kenya, Including a Bird Population Study. By Dale A. Zimmerman. Bull. Am. Mus. Nat. Hist. 149 (3), 1972:255–340, 8 photographs, paper cover. $3.40.—Kakamega forest is a unique island of relict semi-tropical rainforest, with many west African affinities in its flora and fauna unknown elsewhere in Kenya. Many naturalists believe that the forest and its wildlife should be completely protected, for they are endangered by man's activities. "With the present rate of forest destruction," writes Zimmerman, "we are likely to be denied the opportunity to learn."

Zimmerman's work is certainly the first census and population study of this forest, and probably the first population census of any forest in east Africa. He and Alec Forbes-Watson, of the National Museum, Nairobi, have produced a remarkable list of bird species. I was struck, however, by the absence of records of kingfishers in Kakamega. These birds are found in most large East African forests, so I wonder why they are absent here. I was also surprised by the statement that "some of van Someren's records (1922, Nov. Zoo. (Tring) 29:1–246) are difficult or impossible to locate specifically." This difficulty could have been overcome if Zimmerman had personally contacted van Someren in Nairobi.

The methods used to census a 20 acre block within the main forest included spot mapping by sight records, song, play-back recordings, collecting, mist-netting, and banding. The result is an important contribution to ornithology, particularly in East Africa, and a model on which censuses could be based in other East African forests.

Details about mist nets and their use should be heeded by banders. This method of capture can be disastrous in the hands of illegal operators, and nets have been stolen in Kakamega. Netting, however, made possible the recording and recovery of many species, partciularly birds of the understory. These could easily have been missed on visual or sound assessment for, as noted, the songs of *Alethe* and *Sheppardia* were not learned or recorded, and these birds of the forest floor are readily overlooked.

Banding revealed an interesting survival rate, and Zimmerman's data, together with those of other workers netting the same area years later, are impressive. Some birds were recaptured after nearly 4 years in virtually the same spot. A *Cameroptera chloronota*, for example, was taken 5 times between June 1966, and December 1968. The data also demonstrate that there is little movement within a territory over a period

of years. Local Kenyan ornithologists, who freely provided Zimmerman with their records, are continuing to retrap birds that he banded. Recent recoveries, thanks to C. F. Mann of Kapsabet (unpublished), tell more about the life span of these birds and strengthen the belief that they do not wander far from their territories.

Zimmerman comments that in the Kakamega Forest, where the rainfall is 7.6 to 25.4 cm in every month of the year, there was no indication of breeding seasons. He was "surprised by the very few male birds which displayed truly large testes," and quotes Moreau et al. (1946, Proc. Zool. Soc. 117 (2 & 3):345–364) to the effect that "Spermatogenesis commonly takes place in testes that have not attained full size." What is the size of non-active testes, and how much do they enlarge? Measurements are often given to indicate enlargement, but they are meaningless unless the size of the dormant testes is known and quoted for each species.

Flocks of mixed species in the treetops visited the census area but proved difficult to enumerate. Zimmerman simply identified and counted them. *Parus funereus* was a frequent nucleus species, present in 80% or more of the Kakamega parties. Interestingly, Start (1971, Hons. thesis, Univ. of Aberdeen) found *P. albiventris* to be the nucleus species in bird parties in the Karen Forest, near Nairobi, Kenya.

Zimmerman comments on the apparent rarity of bird/ant associations at Kakamega as compared with his observations in Central American forests. In my experience, columns of doryline ants are inconspicuous, but when these ants are spread out and raiding, birds appear in numbers and are always at the front of the raid to capture aroused insects. Evidently Zimmerman did not meet with such raiding parties.

The total number of adult birds in the census area was remarkably uniform in the 3 periods of Zimmerman's study, although the composition and numbers of species varied. The population in 1966 was nearly 25 birds per acre, but we cannot say whether this was high, low, or normal for a forest area until comparable counting is done in other forest regions in East Africa. We really have no knowledge of the carrying capacity of our forests, although this reviewer's 10-acre block of indigenous trees near Nairobi supports 9 breeding residents and 19 transients per acre.

The Kakamega Forest population is indeed impressive, considering the limited period of the observations over 3 visits. Zimmerman comments that an area should be "studied through at least one full year before a true picture of the population can be obtained." His results nevertheless form an excellent basis for future studies. How right is his remark that "even a 500 acre block may represent the minimum area capable of supporting a reasonably natural bird population. Additional study may show this figure to be far too low. Certainly an area so restricted could not maintain itself as a truly natural forest environment indefinitely."

We in East Africa today have no idea what our bird population is, in forest or elsewhere, and little attempt has been made to obtain population statistics on which to base sound conservation measures. Zimmerman's study should be an incentive for others to carry out like studies in all our diverse environments. I am alarmed by the present policy, whereby much indigenous forest is being cut out and replaced by exotic plantations. This affects the whole ecology of an area, and the loss of fauna, flora, and insect life could be devastating and irreparable.

I appreciate Zimmerman's use of the older nomenclature, which generally follows Mackworth-Praed and Grant (1955, Birds of Eastern and North Eastern Africa. African Handbook of Birds, Ser. I, Vol. 2, Longmans, Green and Co., Ltd., London.; 1960, same, 2nd ed.). For example, he maintains *Platysteria* and *Diaphorophia* which

are very different in the field. Also, *Phormoplectes* and *Simplectes* are not lumped under *Ploceus*.

The annotated list of species provides much useful information, but unfortunately some of the fruits, seeds, and flowering plants on which birds were feeding are not mentioned specifically, and data on crop contents are not provided. An interesting analysis could have been made of various bird groups' major food requirements. This could give some indication of the zones exploited from the ground level to treetop.

Zimmerman's comparison of the Kakamega avifauna with that of other forests is striking, as it shows that the Kakamega-Nandi avifauna is one of the richest yet reported for East Africa. Moreau (1966, the Bird Faunas of Africa and its Islands, Academic Press, London) did not include Kakamega in his review.

The report discusses bird habitats, but until more detailed analysis is made, the reasons for associating particular birds with one type of forest remain in doubt. Forests may be similar in number of species of trees and shrubs, but the canopy cover, density, and diversity of understory growth also determine what habitat suits bird species, and this effects the ecology, particularly for the exploitation of food resources.

Zimmerman's study shows that many more coordinated assessments are needed in order to understand all the factors that affect bird populations, and hence the differences in the avifaunas of different forests. This will require time and money to achieve. One resaon for our paucity of ornithological knowledge in East Africa is that virtually all studies in the past 70 years or more was done by amateurs, in their spare time and at their own expense. They have made no mean contribution under the circumstances. Full-time ornithological investigations are needed before it is too late, and Zimmerman's excellent contribution is a more than useful basis for future workers to build upon.—G. R. Cunningham-van Someren.

Feeding Ecology of Pintail, Gadwall, American Widgeon and Lesser Scaup Ducklings. By Lawson G. Sugden. Canadian Wildlife Service Report Series No. 24, 1973: 45 pp. $1.50.

Home Range and Breeding Biology of the Shoveler. By H. J. Poston. Canadian Wildlife Service Report Series No. 25, 1974: 49 pp. $1.50.

Bird Damage to Fruit Crops in the Niagara Peninsula. By R. G. B. Brown. Canadian Wildlife Service Report Series No. 27, 1974: 57 pp. $1.50.

Migration of Lesser Snow and Blue Geese, Part 1. By H. Blokpoel. Canadian Wildlife Service Report Series No. 28, 1974: 30 pp. $1.00.

Migration of Lesser Snow and Blue Geese, Part 2. By H. Blokpoel and Maureen C. Gauthier. Canadian Wildlife Service Report Series No. 32, 1975: 30 pp. $1.00 (Canada), $1.20 (other countries).

These attractively printed, paper-covered reports contain extensive data summarized in tables, charts, and graphs along with the text. Available by mail from Information Canada, Ottawa K1A 0S9, Canada.—R.J.R.

PROCEEDINGS OF THE FIFTY-SIXTH ANNUAL MEETING

James Tate, Jr., Secretary

At the invitation of the Montana State University and the Sacajawea Audubon Society, the 56th annual meeting of The Wilson Ornithological Society was held jointly with The Cooper Ornithological Society. The site of the joint meeting was the modern and comfortable campus of Montana State University in Bozeman, Montana. This second joint meeting of the 2 societies was conducted from 12 through 15 June 1975. The Executive Council of The Wilson Ornithological Society held 2 meetings in a conference room at the Hedges North Residence Hall. Business meetings of The Wilson Society were held in the meeting room in Johnson Hall. These proceedings detail the decisions made, awards presented, papers heard, friends well met, and presentations enjoyed in the beautiful Gallatin Valley of Montana.

A pleasant reception for early registrants was hosted Wednesday evening by the Sacajawea Audubon Society while the Executive Council of The Wilson Society and the Board of Directors of The Cooper Ornithological Society held their separate meetings. On Thursday morning the societies were welcomed in their General Session by Carl W. McIntosh, President of Montana State University. A full day of scientific papers followed. An evening film, Land of Shining Mountains, was presented by Louis M. Moos, photographer and lecturer. Well-organized birding trips were held to nearby localities for the early risers on Friday and Saturday mornings.

Friday's scientific program consisted of a Symposium on Avian Habitats organized by Douglas James. On Friday evening a full schedule of films and slide shows was available to registrants and guests:

(1) The Effects of Airborne Contaminants on Vertebrate Animals, slides by Robert A. Lewis; (2) Some Scenes of Montana Wildlife and Birds of Victoria Island, Northwest Territories, Canada, slides by Alan Nelson; (3) Manana, Island of Birds, color/sound movie courtesy of Robert J. Shallenberger; (4) Some Birds of Northeastern Montana, slides by Charles M. Carlson.

The last day of scientific program was Saturday. A delicious outdoor barbeque was held that evening near a venerable old campus building—The Gray Barn. Awards ceremonies followed by square dancing were then held inside The Gray Barn. On Sunday, many participants returned home; others began extended tours of the west. Throughout the meetings a juried art show of twenty-five Montana artists hung in the Hedges Hall lobby. Registered participants served as the judges of the many outstanding paintings and sculptures.

FIRST BUSINESS MEETING

The first business meeting was called to order by President Parkes at 09:22 Thursday in Johnson Hall, room 339. The minutes of the business meeting held at UMBS, Michigan, were approved by the membership as published in *The Wilson Bulletin* (86:307–320, 1974). The President appointed the *Alexander Wilson Prize* committee with George A. Hall as Chairman. The Nominating Committee was announced as: O. S. Pettingill, Jr., Chairman; H. Lewis Batts, W. W. H. Gunn. The Auditing Committee was announced as: George M. Wickstrom and James F. Ponshair. A joint Wilson-Cooper Resolutions Committee was named with Ronald A. Ryder, Chairman. Reports of officers and committees followed.

REPORT OF THE TREASURER—1974

General Funds

Balance as shown by last report December 31, 1973			$21,023.95
RECEIPTS			
Membership Dues			
Active for 1974	$ 5,205.00		
Active for 1975	8,509.00		
Total Active		$13,714.00	
Sustaining for 1974	360.00		
Sustaining for 1975	450.00		
Total Sustaining		810.00	
Subscriptions to *The Wilson Bulletin*			
For 1974	2,027.00		
For 1975	3,397.00		
Total Subscriptions		5,424.00	
Sales of back issues of *The Wilson Bulletin*		504.95	
Interest and Dividends on Savings & Investments			
Income from General Endowment Fund	5,312.11		
Income from G. M. Sutton Colorplate Fund	1,512.40		
Total Interest and Dividends		6,824.51	
Royalties from microfilming back issues of *The Wilson Bulletin*		174.04	
Total Receipts		$27,451.50	
DISBURSEMENTS			
The Wilson Bulletin (Printing & Engraving)	$17,883.69		
Less contributions from authors & others	0.00		
Printing & Engraving Expense		17,883.69	
The Wilson Bulletin (Additional Mail & Service)		2,822.24	
Editor's Expense		874.16	
President's Expense		89.56	
Review Editor's Expense		45.51	
Secretary's Expense		164.85	
Treasurer's Expense		709.19	
Committee Expense		250.03	
Annual Meeting Expense		388.17	
Transfer to Research and Grants-in-Aid		100.00	
Bank Charges		15.73	
International Council for Bird Protection		30.00	
Miscellaneous Expense		7.00	
Total Disbursements		$23,380.13	
Excess of Receipts over Disbursements			4,071.37
GENERAL CASH FUND			
Checking Account			12,825.90
Savings Account			14,964.80
Balance in Old Kent Bank and Trust Co., Grand Rapids, Michigan, December 31, 1974			$27,790.70

Josselyn Van Tyne Memorial Library Fund

Balance as shown by last report, 31 December 1973	$ 305.78
RECEIPTS	
Sale of duplicates and gifts	422.21
Total Balance and Receipts	$ 727.99
DISBURSEMENTS	
Purchase of books	342.72
Balance in Old Kent Bank and Trust Co., Grand Rapids, Michigan, 31 December 1974	385.27

Louis Agassiz Fuertes Research Fund
Margaret Morse Nice Fund
Edwards and W.O.S. Paper Funds

Balance as shown by last report dated 31 December 1973		$ 195.00
RECEIPTS		
Contributions		1,877.00
Transfer from General Fund		100.00
Total		$2,172.00
DISBURSEMENTS		
Grant-in-aid		
To Storrs Olson	$150.00	
To Joseph Jehl	150.00	
To David Dobkin	200.00	
To Arthur Wiseman	100.00	
To Ralph Babcock	100.00	
Total		700.00
Balance in Old Kent Bank and Trust Co., Grand Rapids, Michigan, 31 December 1974		$1,472.00

Aaron Moore Bagg Student Membership Award Fund

RECEIPTS	
Contributions	$ 200.00
Balance in Old Kent Bank and Trust Co., Grand Rapids, Michigan, 31 December 1974	$ 200.00

Special Fund Account

Balance as shown by last report 31 December 1973		$ 353.25
RECEIPTS		
Prepaid Student Dues	$ 0.00	
Advance Renewels	83.50	
Discount Due Agencies	0.00	
Total Receipts		83.50
Total		436.75

DISBURSEMENTS		0.00
Balance in Old Kent Bank and Trust Co., Grand Rapids, Michigan, 31 December 1974		$ 436.75

Endowment Funds
General Endowment Fund

Balance in Endowment Savings Account as shown by last report, 31 December 1973		$ 16,785.00
RECEIPTS		
Life Membership Payments		5.530.00
Balance in Endowment Savings Account, Old Kent Bank and Trust Co., Grand Rapids, Michigan, 31 December 1974		22,315.00
Investments held as of 31 December 1974		
United States Government bonds	$ 4,925.00	
Canadian Provincial bonds	3,550.00	
Corporate bonds	7,712.50	
Convertible corporate bonds	1,856.25	
Convertible preferred bonds	8,548.13	
Common stocks	34,293.92	
Investment trusts	5,366.12	
Uninvested principal	10.00	
Total Investments		$ 66,261.92
Total General Endowment Fund, 31 December 1974		$ 88,576.92

George Miksch Sutton Colorplate Fund

RECEIPTS		
Contributions		$ 5,000.00
Investments held as of 31 December 1974		
Canadian Provincial bonds	$ 4,400.00	
Corporate Bonds	5,025.00	
Equipment Trust Certificates	8,950.00	
Common stocks	1,725.00	
Uninvested principal	1,554.85	
Total Investments		$ 21,654.85
Total, Combined Wilson Ornithological Society Endowment Funds, 31 December 1974		$110,231.77

Ernest E. Hoover, *Treasurer*

REPORT OF THE EDITOR—1974

Since becoming editor in June 1974, I have received 246 manuscripts plus book reviews, news items, and the President's Page. Some of the 246 manuscripts were revisions initially received under the previous editor, but the bulk was new. During this same time period last year, John Hubbard had received 194 manuscripts. As of the date of this report, the fates of the manuscripts I have received have been as follows: pub-

lished, 46; in press, 25; accepted, 40; out for refereeing, 29; returned for revision, 49; rejected, 57.

Processing time was calculated from time of receipt of any original manuscript (including those revised under the previous editor) to acceptance: 50 papers published (March, June) or in press (September)—120.6 days, S.D. = 82.5 days; 58 notes (same specifications) 76.3 days, S.D. = 43 days. Based on 3.5 months in press time, the lead time can be put at about 12 months for a paper and just under 12 months for a note. . . and rising! As might be expected, it takes less time to have a paper rejected than it does to have one accepted. Of 55 manuscripts rejected (notes and papers combined) time from receipt to rejection averaged 47.8 days, S.D. = 70.0. The rejection rate this past year was 26.3%, compared to 19.9% for 1974, 31.6% for 1972, 30.0% for 1971, and about 27% for the 1974 Auk.

Due to cost increases, page charges for *The Wilson Bulletin* will be immediately raised to $40. Page charges must be paid for all printed pages in excess of 20. In addition, authors willing to pay all page charges will have their manuscripts published in the next available issue. Such manuscripts will be published in addition to those regularly scheduled for publication.

Time out to referees continued to be reasonably good—averaging 21.0 days, S.D. = 17.5 for all manuscripts. I am grateful to the 211 people who have refereed manuscripts for *The Wilson Bulletin* during the past year.

Jerome A. Jackson, *Editor*

REPORT OF THE RESEARCH COMMITTEE—1974

Your Committee recommends that the 1975 Fuertes Award go to Ms. Margaret Elsie McVey c/o R. Case, RFD 1, Box 176, Stovington, Connecticut 06378. The title of her research project is: The Social Dynamics of a Loosely Colonial Passerine, the Barn Swallow (*Hirundo rustica*). This project is extremely well conceived and will emphasize the role of vocalizations in the social behavior of this species. Ms. McVey received outstanding letters of recommendation from several well-known ornithologists and she seems a most promising student.

If it is possible to give 2 Fuertes Awards this year, the Committee recommends that a second award go to Mr. Roger L. Boyd whose address is 622 South Taft Hill Road, Fort Collins, Colorado 60521. His research project is entitled: Energy and Food Biomass of the Horned Lark on the Shortgrass Prairie. Mr. Boyd's research proposal was an unusually detailed and competent one. He too had strong letters of support and was tied with McVey in the final rankings of the Committee. However, we chose to give McVey first place because she has not received any other financial assistance for her project. In contrast, Boyd has received some support from other sources.

Twelve people completed the application process, i.e., did more than write letters of inquiry or request forms. These applications were of exceptionally high quality. Most of the Committee members commented on the difficulty of the rankings and how deserving of support were most of the proposals.

Your Committee recommends that the 1975 Nice Award go to Jerome J. Barry of Woodland Road, Apartment 8, Merrimack, New Hampshire 03054. Mr. Barry's proposal was entitled: Avian Ectoparasites: Their Biology and Importance as Disease Vectors. This proposal was an extremely broad one but if he achieves only part of his objective it will be an important contribution.

The number of applications for the Nice Award was up this year. We had 5 applicants, although 2 of these had dubious "student" status.

Frank B. Gill, *Chairman*

REPORT OF THE EDWARDS PRIZE COMMITTEE—1974

The decision of the Edwards Prize Committee on selection of the first and second best papers in Volume 86 of *The Wilson Bulletin* is:

First Prize: William E. Southern, The effects of superimposed magnetic fields on gull orientation, pp 246–271. Second Prize: Rodman Ward and Dorcas A. Ward, Songs in contiguous populations of Black-capped and Carolina chickadees in Pennsylvania, pp 344–356.

FRANCES C. JAMES, *Chairman*

REPORT OF THE MEMBERSHIP COMMITTEE—1974

At its last annual meeting the society decided that the publication of the membership list would become a duty of the Membership Chairman. That task occupied much of my time last fall. I made several changes in the format in which the list is presented. Of these, 2 are important. First, Sustaining Members are not designated. The Treasurer indicates that sustaining membership changes from year to year, evidently influenced by the affluence of our membership. Hence, Sustaining Members are not in quite the same category as Patrons or Life Members. It does seem appropriate, however, that the society find some way to indicate its appreciation of the generosity of these people, and I would suggest publication of an annual list of Sustaining Members.

Second, I added a geographical index (by zip code). This was done primarily upon consideration that many of our members are amateurs and might like to be able to locate others with similar interests in their area. I would greatly appreciate learning how many members do find this feature useful as it does require extra pagination and expense, and it is some trouble to maintain a dual listing of the membership.

This year we have added 180 members while losing, for a variety of reasons, 150, for a net gain of 30 new members. For the third consecutive year we have recruited more individuals than we have lost. The new members come from 42 of the United States, Washington, D.C., Puerto Rico, 6 of the Provinces of Canada, and 7 other foreign countries. They have been recommended by 55 members of the society.

In hopes of being able to direct future recruiting campaigns, I attempted to ascertain who leaves the society. My analysis includes all losses not due to death and assumed that such losses are permanent despite the fact that some of those lost for nonpayment of dues (the largest category) and many who have moved without yet sending a new address will be reinstated. The class of 1974, which was previously analyzed for "who joins", was considered in some detail.

A chart of members lost, plotted against year of joining, closely resembles similar charts of losses in populations of small passerines. The first year includes 28.9% of the losses, while 54.2% occur within the first 5 years and 71.8 within the first 10. We expect that some new recruits, finding that the society is not what they had in mind, will leave rapidly. A peculiar bulge in drops about year 10 may represent marginal members for whom the present economic situation is a deciding factor.

Thirty-three (19.1%) of the 173 members upon which last year's report was based left the society. The losses were remarkably evenly distributed through most of the classes analyzed (18% of the males, 23% of females, 19% of students recruited). Only 2 groups were exceptional. Losses were high among non-ornithological, professional biologists (33%) and low among educators (4%). These data suggest that "loyalty" is an unpredictable factor. Hence, little would be gained by directing our recruiting to specific groups.

A. S. GAUNT, *Chairman*

REPORT OF THE CONSERVATION COMMITTEE—1974

Four specialists, Maurice F. Baker, Jay S. Gashwiler, Robert L. Eng, and Max H. Schroeder, were asked to consider the committee's chosen topic. Their report, The Effects of Alteration of Sagebrush Communities on the Associated Avifauna, was prepared and submitted to the Council of The Wilson Ornithological Society. It will be published in *The Wilson Bulletin* in 1976. The Conservation Committee asks the Council for guidance on future topics for consideration.

CLAIT E. BRAUN, *Chairman*

REPORT OF THE LIBRARY COMMITTEE—1974

This report covers specifically the period 1 June to 31 December, 1974, and subsequent annual reports will apply to calendar years.

The past year has been one of rather more than the usual upheaval, as regards both personnel and University Library procedures. Our basic aims remain unchanged; it is hoped that members can use the growing collections to even better advantage and will take increased interest in adding to them.

Gifts received included 154 books, 473 periodicals, 25 reprints, and 27 pamphlets, from 7 donors. The fine bequest from the library of the late C. Chandler Ross constituted some 84% of the total gifts for the period.

Outside loans, to 13 members, involved 23 separate items.

A total of $55.00 realized from the sale of duplicate books and other items went into the New Book Fund to help with library acquisitions.

Somewhat belatedly, thanks are extended to Sheldon Miller for his years of service to the Josselyn Van Tyne Memorial Library. We welcome Janet Hinshaw, who now holds the position of Technician in the U.M.M.Z. Bird Division and is already ably coordinating the many details of our work.

WILLIAM A. LUNK, *Chairman*

Lists of new members were posted in the meeting hall by the Secretary. Announcements were made that the 57th Wilson Ornithological Society Meeting is planned for Cornell University from 3 through 6 June 1976, and the 58th Wilson Ornithological Society Meeting is planned for Mississippi State University from 18 through 21 May 1977. There being no further business, the President closed the first business meeting at 10:12.

SECOND BUSINESS MEETING

President Parkes called the meeting to order at 16:05 on Saturday. A report on proposed amendments to the constitution of The Wilson Ornithological Society was made by President Parkes. He detailed many of the proposed amendments that have been accepted by the Council. The most recent Constitution and Bylaws of The Wilson Ornithological Society were adopted 29 December 1930, and amended by the Executive Council on 11 August 1944, and 13 October 1945. The then revised Constitution and Bylaws were approved by the membership on 29 November 1946, and amended September 1951 (by mail ballot), and 9 April 1955. The full amended and revised Constitution and Bylaws were published in *The Wilson Bulletin* (67:224–226, 1955). The following amendments were approved by unanimous vote of the assembled council with only a single abstention on one motion at its meeting on 12 June 1975.

Article I, Section 2, and Article II, Section 2.

References in these articles should be to "Objective" rather than "Object."

Article I, Section 1.

Add the following as a second and third sentence:

It shall be registered under that name as a Corporation in an appropriate state, fulfilling any requirements for incorporation under the laws of that state. If the state in which the Corporation is registered should impose new requirements that conflict with the objectives or the financial means of the Society, the Board of Directors of the Corporation may dissolve the Corporation and reincorporate under the laws of another state.

Article I, Section 2.

Delete: " . . . , particularly field ornithology as related to the birds of North America."

Article II, Section 2.

Delete: ". . . of good moral character and . . ."

Note from the Secretary: Also notice that I have changed the word object to objective in this section so that it is consistent with the title of Article I.

Article II, Section 3.

Substitute the following wording:

"The Executive Council shall determine the amount of the dues for Active and Sustaining Members, of institutional subscriptions to *The Wilson Bulletin*, and of payments into the endowment fund of the Society to qualify for the classes of Life Member and Patron. Persons desiring to become Life Members or Patrons may, if they wish, pay one quarter of the amount set for these classes into the endowment fund in four consecutive annual installments.. They are then exempt from further dues. Upon the unanimous recommendation of the Executive Council, honorary membership may be conferred by the Society by a three-fourths vote at any annual meeting." Also to remove existing Bylaw #8.

Article II, Section 5.

Delete: ". . . for one year . . ."; and insert ". . . at least . . ." before the words ". . . two months . . ." in the second sentence.

Article III, Section 1.

Substitute for ". . . two Vice-Presidents . . ." the phrase ". . . a First Vice-President, a Second Vice-President . . ."

Article III, Section 2.

Substitute in part the wording of Bylaw #4 as the body of this section so that it reads as follows:

All officers and elected members of the Executive Council, except the Editor, shall be elected at the annual meeting by ballot of the members. By the unanimous consent of the members, the Secretary may cast one ballot, representing the unanimous vote of the members present. A nominating committee composed

of three or more members shall be appointed by the President at the beginning or in advance of the annual meeting, which shall offer nomination of officers and elected members of the Executive Council to serve the Society during the ensuing year. Nominations may also be made by any member in good standing from the floor. The Editor shall be elected annually by the Executive Council. Also to remove the current Bylaw #4.

Article III, Section 3.

To cause existing Bylaw #13 to become Article III, Section 3, and to renumber remaining sections in Article III. Also to remove current Bylaw #13.

Article III, Section 3. (New Section 4 with the adoption of the above change.)

Substitute the following wording:

The President and the two Vice-Presidents shall hold office for one year or until their successors are elected, and shall be eligible for re-election for a second year. Upon retirement of the President, the First Vice-President shall be nominated for President and the Second Vice-President for First Vice-President, unless otherwise determined by the Nominating Committee. The Secretary, Treasurer, and Editor are eligible for re-election indefinitely. Terms of office shall begin at the close of the meeting at which the officers were elected.

Article III, Section 4. (New Section 5 with adoption of the above change.)

Add as second sentence:

"The term of office for the three elected members of the Executive Council shall be three years, without re-election, with terms staggered so that the term of one such member expires each year."

Article IV.

Add the words "regular annual" before ". . . meetings of the Society." in Section 1, and add the words ". . . at regular annual meetings." at the end of Section 2.

Article V, Section 1.

Drop the words ". . . of two . . ." after the word "committee".

Article V, Section 2.

Remove the reference to terms for a Board of Trustees by deleting everything following the word President in the second sentence, and all of the third and fourth sentences.

Article VI, Section 1.

Add the word "regular" to the phrase "annual meeting" and delete the word "voting".

Article VII, Section 1.

Add at the end of the sentence: ". . . , provided that a copy of the suggested changes has been mailed to every member of the Society at least one month prior to regular annual meeting."

Bylaw 3.

Delete after "A program committee . . ." the words ". . . of which the Secretary shall be chairman . . .", and add the word "scientific" before the word "program".

Bylaw 5.

Delete the words ". . . consisting of three members".

Bylaw 6.

Delete the words ". . . one or more . . ." and substitute the article ". . . a . . ." in their place. Change "libraries" to the singular. In the second sentence, delete the phrase ". . . of three or more members . . ."

Bylaw 8.

To become in total Article I, Section 3 (new section).

Bylaw 9.

Remove this bylaw.

Bylaw 11.

Substitute the following wording for the introduction: "The agenda at regular annual meetings shall include: . . ." Also delete the last sentence.

Bylaw 14.

Change the first sentence so that it begins: "This constitution and bylaws may also be amended . . ."

The preceding amendments will be brought to a vote of the members present at the next regular annual meeting of The Wilson Ornithological Society.

The following report of the Auditing Committee was accepted:

REPORT OF THE AUDITOR—1974

We the undersigned have examined and verified the books, records, and bank statements under the care of the Treasurer, Ernest E. Hoover, and find them in agreement with the Annual Report for 31 December 1974. We are satisfied that the books accurately present the financial condition of the Wilson Ornithological Society at close of business 31 December 1974.

George M. Wickstrom, James F. Ponshair, *Auditing Committee*

The Secretary called for a vote to accept the list of proposed members of The Society as posted. Motion to accept the persons named on said list was made, seconded, and passed by voice vote. O. S. Pettingill, Jr., Chairman of the Nominations Committee, proposed the following slate of officers: For President, Andrew J. Berger; First Vice-President, Douglas A. James; Second Vice-President, George A. Hall; Secretary, James Tate, Jr.; Treasurer, Ernest Hoover; Elective Member of the Council (3 years), Abbot S. Gaunt; Elective Member of the Council (unexpired 1-year term), A. J. Erskine. There being no further nominations from the floor, nominations were closed. The membership directed the Secretary to cast a unanimous ballot for the proposed slate.

REPORT OF THE JOINT RESOLUTIONS COMMITTEE

The following resolutions were read and passed at the joint session of the two Societies:

WHEREAS, the Cooper Ornithological Society and the Wilson Ornithological Society have assembled in their joint annual meeting at Bozeman, Montana 12–15 June 1975 and

WHEREAS, the members of the two societies have benefited greatly from the dedicated efforts of the committee on arrangements chaired by Clifford Davis, and

WHEREAS, the excellent services, facilities, and hospitality provided by Montana State University have contributed immeasurably to the success and enjoyable nature of this jointing meeting,

THEREFORE, BE IT RESOLVED that the Cooper and Wilson Societies extend their grateful appreciation to the sponsoring organizations, Montana State University and the Sacajewea Audubon Society.

BE IT RESOLVED that the Cooper Ornithological Society and the Wilson Ornithological Society recommend that the Secretary of the Interior and the Director of the U.S. Fish and Wildlife Service request the assistance of a group of qualified zoologists as the basis for the granting of permits for scientific collection of birds rather than delegating responsibility for approval or disapproval of such permit requests entirely to the Law Enforcement Division of the U.S. Fish and Wildlife Service.

WHEREAS, many of the members of the Cooper and Wilson Ornithological Societies have conducted avian research in the Gulf of California and on the Peninsula of Baja California, and

WHEREAS, recent developments and activities in those areas pose serious threats to the well-being and survival of many birds there,

THEREFORE, BE IT RESOLVED that the Cooper and Wilson Societies endorse the Pacific Seabird Groups Policy Statement No. 1, of 1 May 1974 concerning "Seabird Conservation in the Gulf of California", and

BE IT FURTHER RESOLVED that written endorsement be submitted herewith to the Government of Mexico.

WHEREAS, the Cooper and Wilson Ornithological Societies represent an important cross section of the scientific community concerned with the serious study and conservation of birds in the United States, and

WHEREAS, the Kileuea Forest Preserve on the Island of Hawaii and owned by the Bernice Pauahi Bishop estate is valuable habitat for at least 4 species of endangered birds, the Io (Hawaiian hawk, *Buteo solitarius*), *the Akiapola'au* (*Hemignathus wilsoni*), the Hawaii 'Akepa (*Loxops coccinea coccinea*), the Hawaii creeper (*Loxops meculapa mana*) and possibly a 5th endangered species, the O'u (*Psittirostra psittazea*) and

WHEREAS, the B. P. Bishop estate plans to clear and log 200 acres of this valuable habitat, and

WHEREAS, this proposed habitat operation will apparently be a violation of the intent and purposes of the federal Endangered Species Act of 1973,

THEREFORE, BE IT RESOLVED that the Cooper and Wilson Ornithological Societies urge the Board of Trustees of the B. P. Bishop estate to reconsider their proposed plans for logging and only permit logging to the extent as recommended by the Office of Endangered Species of the U.S. Fish and Wildlife Service in order to provide adequate habitat for the above-mentioned species of endangered birds.

RONALD A. RYDER, *Chairman*

The President closed the second business meeting at 16:30.

ATTENDANCE

From ALASKA: *Fairbanks*, Brina Kessel.

From ARIZONA: *Flagstaff*, R. P. Balda, Michael Salomonson, Robert C. Szaro; *Prescott*, Carl Tomoff; *Tempe*, Wm. Flaudeslan, Judd Howell, Wm. F. Landenslayer, Robert D. Ohmart, Nancy Stamp; *Tacson*, Dorothy Russell, Stephen M. Russell.

From ARKANSAS: *Fayetteville*, Peter A. Money, Alan F. Posey, Brenda Posey, Richard Thomas; *Little Rock*, Henry Halberg, Edith Halberg.

From CALIFORNIA: *Albany*, T. James Lewis, Barbara Lewis; *Alta Loma*, Fredda Fox, *Arcata*, Howard Levenson; *Berkeley*, Stephen F. Bailey, Oliver Pearson, Anita Pearson, Jennifer White; *Cholame*, Eban McMillan, Gladys McMillan; *La Jolla*, Granville Hatch; *Larkspar*, Robert Orr; *Long Beach*, Charles T. Collins; *Los Angeles*, Ed N. Harrison, Henry Hespenheide, Thomas R. Howell, Richard L. Hutto, Sandra Jones, Kenneth E. Stager; *McKinleyville*, James R. Koplin, Kitchen Koplin; *Northridge*, Bill Boarman; *Oakland*, Enid Austin, Jane R. Durham; *Orange*, Steve Sanders; *Placentia*, Ray Munson, Barry Thomas; *Sacramento*, Tim Mabolis; *San Diego*, Gerald Collier; *San Francisco*, L. C. Binford; *San Jose*, Rebecca Marchello; *San Mateo*, Joseph Hall; *Santa Barbara*, B. B. DeWolfe, Dennis M. Power, Diana Tomback; *Saratoga*, Diana G. Matthiesen; *Seal Beach*, Cliff Hill; *Stanford*, Timothy Szaro; *Van Nuys*, Nicholas Collias, Mrs. N. Collias, William Issler.

From COLORADO: *Boulder*, Jeanne A. Conry; *Colorado Springs*, James H. Enderson; *Denver*, Marcie Meierkord, Jim Neal; *Fort Collins*, Paul H. Baldwin, Clait E. Braun, Nancy Braun, James R. Rees, Ronald Ryder; *Golden*, James Tate, Jr., D. Jean Tate; *Lakewood*, Charles P. Stome; *Northglenn*, Walter Graul.

From DELAWARE: *Wilmington*, David Niles, Mr. and Mrs. Rodman Ward.

From FLORIDA: *Gainesville*, John William Hardy; *Lakeland*, John R. Haldeman; *Tampa*, Mercedes Foster, *Winter Haven*, Peggy MacQueen.

From HAWAII: *Honolulu*, Andrew J. Berger, Sheila Conant.

From IDAHO: *Boise*, Thomas C. Dunstan, James F. Harper; *Courdelene*, Ron McDow; *Kamiah*, Jeffrey Hughes; *Moscow*, Wayne E. Melquist; *Pocatello*, Michael Delate, Ronald Sehman, Charles H. Trost, Wayan Drewien.

From ILLINOIS: *Carbondale*, Wm. S. George, Martin Kemper, Tim Kimmel, Daniel Klem, Renee Klem, Eugene LeFebvre; *Champaign*, George Kulesza; *Chicago*, Joel Cracraft, Bill Lukshia; *Cottage Hills*, Mr. and Mrs. Harold E. Broadbrooks; *Momence*, W. Lory, Hazel Lory, Mrs. Edith Reid; *Marphysboro*, Gary L. Nunn.

From INDIANA: *W. Lafayette*, James R. Karr, Kathleen Karr.

From KANSAS: *Lawrence*, Robert S. Hoffmann, Robert Mengel, Marion Mengel.

From LOUISIANA: *Baton Roage*, Robert B. Hamilton.

From MAINE: *Kirksville*, Barbara Harris; *Wayne*, Mr. and Mrs. O. S. Pettingill.

From MARYLAND: *Gaithersberg*, Douglas James; *Odenton*, Danny Bystrak.

From MASSACHUSETTS: *Middleboro*, Paul Anderson, Kathleen Anderson.

From MICHIGAN: *Ann Arbor*, Cynthia Carey, Wm. R. Dawson, Virginia Dawson, Hank Howe, Ronald I. Orenstein, Robert Payne, Robert Storer; *Grand Rapids*, Ernest Hoover; *Mt. Pleasant*, Robert Peterson.

From MINNESOTA: *Collegeville*, N. L. Ford; *Dalath*, Mr. and Mrs. P. B. Hofslund; *Minneapolis*, Walter Breckenridge, Dorothy Breckenridge, Douglas Mock, H. B. Tordoff, N. Tordoff.

From MISSISSIPPI: *Mississippi State*, Jerome A. Jackson.

From MISSOURI: *Colambia*, Wm. H. Elder, Glennis Elder, Keith Evans; *Cape Girar-*

deau, Wm. R. Eddleman; *Puxico*, Leigh H. Fredrickson, Judy Fredrickson; *Raytown*, Mark S. Taylor; *St. Louis*, Norman Woldow.

From MONTANA: *Ashland*, M. L. Morton; *Belgrade*, Jerry Light; *Billings*, Mrs. C. H. Bjoran, Bebe FitzGerald, J. H. Phelps, Bill Rone; *Bozeman*, Ron Batchelor, Clyde H. Border, Ellamay Border, Nina Bradley, Merrill Burlingame, Virginia Burlingame, Helen Carlson, Grace M. Carney, Cliff Davis, Toots Davis, Cy D. Evans, Betty Evans, John Fisher, Dorothy Fisher, Dennis S. Flath, Mary Geis, Raymond A. Hays, Eva Hays, H. N. Metcalf, Henry Montagne, Louis Moos, Opal Moos, John C. Prange, P. D. Skaar; *Butte*, Lila Laity; *Clancy*, Vincent Yannone; *Ft. Peck*, Charles M. Carlson, John Carlson; *Gallatin Gateway*, Dorothy P. Nile; *Great Falls*, Alan Nelson; *Hamilton*, Marc Bielenberg; *Helena*, Jean Smith, Larry S. Thompson; *Joliet*, Billie Hicks; *Lewistown*, Anna Zellick; *Missoula*, Patricia A. Baird, Joan Bird, Burr J. Betts, Anthony Caprio, Patricia M. Dolan, Don Jennie, James A. Sedgwick, Barry Storer, Phil Wright; *Wilsall*, Florence Wegener, Victor Thornbrugh.

From NEBRASKA: *Omaha*, Wm. A. DeGraw.

From NEW HAMPSHIRE: *Lebanon*, Peter Stettenheim.

From NEW JERSEY: *Chester*, C. B. Schaughency; *Mt. Holly*, Katherine Price; *New Brunswick*, Charles Leck.

From NEW YORK: *Armonk*, Michael Kern; *Ithaca*, Sam E. Weeks; *New York City*, Chris Doner, Eugene Eisenmann, L. L. Short, Stuart Keith and Mrs. Stuart Keith; *Syracuse*, Harry W. Power.

From NORTH CAROLINA: *Greensboro*, Charles Black.

From NORTH DAKOTA: *Jamestown*, Douglas Johnson.

From OHIO: *Columbus*, Abbot Gaunt and Mrs. Abbot Gaunt, Thomas C. Grubb; *Lakewood*, Wm. A. Klamm; *Sandusky*, Allen Stickley; *Toledo*, J. M. McCormick, Luella McCormick; *Waterville*, Harold F. Mayfield.

From OKLAHOMA: *Norman*, Joseph Grzybowski, Jenna Hellack, Gary Schnell, Mary Sue Schnell; *Tecumseh*, D. Schott Wood.

From OREGON: *Ashland*, John O. Sullivan; *Burns*, Carroll D. Littlefield; *Corvallis*, Robert A. Lewis; *Portland*, Robert Grimm.

From PENNSYLVANIA: *Audubon*, Wm. T. Tucker; *Chester Springs*, Mr. and Mrs. Phillips B. Street; *New Ringgold*, Mr. and Mrs. Maurice Broun; *Pittsburgh*, Doug Kibbe, Kenneth Parkes; *Carlisle*, C. John Ralph, Carol Ralph; *Ulster*, Erika Wilson; *University Park*, David Pearson, Fred Samson.

From SOUTH CAROLINA: *N. Augusta*, Robert W. McFarlane; *Seneca*, Robert G. Hooper, Joan Hooper.

From SOUTH DAKOTA: *Rapid City*, L. M. Baylor, Roger Kerbs, Harold Messner, Dr. and Mrs. N. R. Whitney; *Sioux Falls*, Brent Hagland, Dayle Hagland; *Spearfish*, Thomas M. Hays.

From TENNESSEE: *Maryville*, Ralph J. Zaenglein.

From TEXAS: *Austin*, Mr. and Mrs. Charles Hartshorne; *College Station*, Brian W. Cain; *Huntsville*, Ralph R. Moldenhaver.

From UTAH: *Logan*, Robert Clemans, Bob Flynn, James Gessaman, Steven R. Hays, Kimberly Smith, Jan Young; *Ogden*, Carl Marti, Al Theis; *Orem*, Herbert H. Frost; *Provo*, Joseph Murphy, Bob Whitmore; *Salt Lake City*, Wm. H. Behle, Brooke Stiling.

From VIRGINIA: *Richmond*, C. R. and Leann Blem; *Williamsburg*, Ruth A. Beck, Susan C. Sturm.

From WASHINGTON: *Big Harbor*, Gerald V. Tamgrem; *Pullman*, Richard E. Johnson; *Seattle*, Karl Kenyon, David A. Manuwal, Naomi Manuwal, Gordon H. Orians, Sievert Rohwer, Chris Servheen, Jan P. Smith, Doug Wood, Robin Wood.

From WEST VIRGINIA: *Morgantown*, George A. Hall.

From WISCONSIN: *Madison*, Michael Jaeger, Robert McCabe, Marie McCabe; *Milwaukee*, Daniel D. Berger, Owen Royce; *Oshkosh*, Michael Minock.

From AUSTRALIA: *Turramurra*, Murray D. Bruce.

From BRAZIL: *Glamado*, Wm. Belton, Julia Belton.

From CANADA: *Alberta*, Wm. Gunn, M. T. Myres, Don Pattie; *British Columbia*, N. A. Din, Nico Verbeek, Wayne Weber, Wendy Weber; *Ontario*, Jake Rice, W. John Richardson, Dorothy Richardson; *Saskatchewun*, Wm. J. Maher.

From COSTA RICA: Susan Smith.

Others in attendance: Patricia G. Brown, Ellie D'Arms, Kathleen E. Franzreb, Jeff C. Holder, Jeri Paulson, Steven Ray, Edgar Stone, Gary L. Worthen, Kathie Worthen.

PAPERS SESSIONS

P. D. Skaar, Montana State University, Bozeman, Montana, *Mapping Montana Bird Distribution by Latilong.*

Ronald A. Ryder, Colorado State University, Fort Collins, Colorado, *Population Trends of Some Common Breeding Birds in Colorado.*

Nancy Stamp, Arizona State University, Tempe, Arizona, *Densities of Overwintering Birds Along the Salt and Verde Rivers, Maricopa County, Arizona.*

James H. Enderson, Colorado College, Colorado Springs, Colorado, and Jerry Craig, Colorado Division of Wildlife, Denver, Colorado, *Status of the Peregrine Falcon in the Rocky Mountains.*

Wayne E. Melquist and Donald R. Johnson, University of Idaho, Moscow, Idaho, *Present Status of Ospreys in Northern Idaho and Northeastern Washington.*

Patricia A. Baird, University of Montana, Missoula, Montana, *Comparative Ecology of Ring-billed and California Gulls.*

Michael D. Kern, Fordham University, Bronx, New York, *Nest Construction by Canaries —Is the Incubation Patch Involved?*

Robert W. McFarlane, Savannah River Ecology Laboratory, Aiken, South Carolina, *Noncyclic Reproduction of Sooty Terns on Wake Island.*

Leigh H. Fredrickson and James L. Hansen, Gaylord Memorial Laboratory, University of Missouri, Puxico, Missouri, *Second Broods in Wood Ducks.*

James A. Sedgwick, University of Montana, Missoula, Montana, *A Comparative Study of the Breeding Biology of Hammond's and Dusky Flycatchers.*

William J. Maher, University of Saskatchewan, Saskatoon, Saskatchewan, *Diet of Nestling Prairie Passerines at Matador, Saskatchewan, Canada.*

Charles F. Leck and Martha S. Hughes, Rutgers University, New Brunswick, New Jersey, *The Influence of Environment on the Nestling Feeding Rate of the Tree Swallow.*

Allan B. Crockett, University of Colorado, Boulder, Colorado, *Feeding Ecology of the Williamson's Sapsucker in Colorado.*

Richard E. Johnson, Washington State University, Pullman, Washington, *Comparative Feeding Ecology of Two Populations of Rosy Finches in Contrasting Habitats.*

Michael G. Salomonson, Northern Arizona University, Flagstaff, Arizona, *The Effects of Food Availability on Winter Territorial Behavior of Townsend's Solitaries.*

Nicholas A. M. Verbeek, University of British Columbia, Vancouver, British Columbia, *Northern Wintering of Flycatchers and Residency of Black Phoebes.*

Wayne C. Weber, 170 East Fourth Street, North Vancouver, British Columbia, *Foraging Ecology of Urban Birds in Vancouver, British Columbia.*

William F. Laudenslayer, Jr., Arizona State University, Tempe, Arizona, *Seasonal Shifts in Avian Utilization of Tree Species and Foraging Heights in Three Mixed Mesquite Communities.*

C. John Ralph, Dickinson College, Carlisle, Pennsylvania. *Determination of Circadian Timing of Migrants.*

James F. Harper and Thomas C. Dunstan, Western Illinois University, Macomb, Illinois, *Dispersal and Migration of Fledgling Bald Eagles.*

Thomas C. Dunstan and James F. Harper, Western Illinois University, Macomb, Illinois, and John E. Mathisen, Chippewa National Forest, Cass Lake, Minnesota, *Behavior and Habitat Use of Fledgling Bald Eagles in North Central Minnesota.*

Diana F. Tomback, University of California, Santa Barbara, California, *Pre-roosting Flights of the Clark's Nutcracker in the Eastern Sierra Nevada: Phototaxis or Thermoregulation?*

Russell P. Balda and Michael L. Morrison, Northern Arizona University, Flagstaff, Arizona. *Roosting Behavior of the Piñon Jay.*

Carl D. Marti, Weber State College, Ogden, Utah, *Prey Selection in the Long-eared Owl.*

Thomas C. Grubb, Jr., Ohio State University, Columbus, Ohio, *Discrimination of Flying Predators by American Coots in Nature.*

Daniel Klem, Jr. and Gary L. Nunn, Southern Illinois University, Carbondale, Illinois, *Adaptive Significance of Certain Predatory Behavior Patterns and Their Sequencing in the American Kestrel and Red-tailed Hawk.*

Gary L. Nunn, Southern Illinois University, Carbondale, Illinois, *A Predictive Model for Occurrence of the Fixed Action Pattern "Killing Bite" in the American Kestrel.*

Susan M. Smith, Universidad de Costa Rica, Ciudad Universitaria, Costa Rica, *Prey-attack Behavior by Young Turquoise-browed Motmots.*

Brent M. Haglund, Augustana College, Sioux Falls, South Dakota, *Breeding Bird Communities of Northern Rocky Mountain Vegetation Types.*

Clait E. Braun, Colorado Division of Wildlife, Fort Collins, Colorado, *Seasonal Habitat Selection by White-tailed Ptarmigan.*

Jerome A. Jackson, Mississippi State University, Mississippi State, Mississippi, *Colony Site Selection, Use, and Abandonment by the Red-cockaded Woodpecker.*

John R. Haldeman, Florida South College, Lakeland, Florida, *Junco Habitats in the Western United States.*

James C. Rice, University of Toronto, Toronto, Canada, *Habitat Cooccupancy in Two Interspecifically Territorial Vireos.*

Gordon H. Orians, University of Washington, Seattle, Washington, *Marshes as Breeding Environments for Passerine Birds.*

Donald H. White, Patuxent Wildlife Research Center, Laurel, Maryland, *Environments of Freshwater Feeding Sites of Waterfowl in Autumn on the Welder Wildlife Refuge in Southern Texas.*

Carl S. Tomoff, Prescott Center for Alternative Education, Prescott, Arizona, and Stephen M. Russell, University of Arizona, Tucson, Arizona, *Desert Bird Communities and Their Vegetational Habitats.*

George Kulesza, University of Illinois, Urbana, Illinois, *Breeding Bird Diversity in Structurally Simple Habitats: Responses to Vegetation Growth.*

Bertin W. Anderson and Robert D. Ohmart, Arizona State University, Tempe, Arizona, *Birds of Three Plant Communities in the Lower Colorado River Valley.*

Robert C. Whitmore, Brigham Young University, Provo, Utah, *Habitat Partitioning in Birds of the Riparian Community of Southwestern Utah.*

Douglas James, Energy Research and Development Administration, Washington, D.C., *Vegetational Habitats of African Shrubland Birds.*

Alan F. Posey, University of Arkansas, Fayetteville, Arkansas, and Douglas James, Energy Research and Development Administration, Washington, D.C., *Habitat Partitioning by Shrubland Birds in Arkansas and West Africa.*

Robert C. Szaro and Russell P. Balda, Northern Arizona University, Flagstaff, Arizona, *The Effects of Seasonality on Bird Communities in the Ponderosa Pine Forest.*

Kimberly G. Smith, University of Arkansas, Fayetteville, Arkansas, *Distribution of Summer Birds Along a Forest Moisture Gradient in an Ozark Watershed.*

Sheila Conant, University of Hawaii, Honolulu, Hawaii, *Avian Population Dynamics in Some Hawaiian Habitats.*

Henry A. Hespenheide, University of California, Los Angeles, California, *A Comparison of Bird Community Structure in Two Panama Forests.*

David L. Pearson, Pennsylvania State University, University Park, Pennsylvania, *The Relation of Bird Community Structure to Foliage Complexity on Three Amazonian Plots.*

James R. Rees, 509 Skyline Drive, Fort Collins, Colorado, *Breeding Behavior of Marsh Hawks in Arid and Mesic Grassland Habitats.*

Thomas R. Howell, University of California, Los Angeles, California, *Reproductive Adaptations in the Blue-footed Booby.*

B. J. Betts and D. A. Jenni, University of Montana, Missoula, Montana, *Parental Behavior of Female American Jacanas.*

Charles H. Black, 2707 Pinelake Drive, Greensboro, North Carolina, *Reproductive Strategies of Female Spotted Sandpipers.*

Douglas W. Mock, University of Minnesota, Minneapolis, Minnesota, *Vocabulary Shifts During Pair-formation in Great Blue Herons.*

Robert B. Payne, University of Michigan, Ann Arbor, Michigan, *Mating Systems and Intra- and Inter-sexual Selection in a Population of Non-parental Birds.*

Mercedes S. Foster, University of South Florida, Tampa, Florida, *Male-male Pairs and Reproduction in the Long-tailed Manakin.*

Sievert Rohwer, University of Washington, Seattle, Washington, and David M. Niles, Delaware Museum of Natural History, Greenville, Delaware, *Plumage Variability, Female Mimicry and 100 Years of Evolution in Subadult Purple Martins.*

John R. Watson, University of New Mexico, Albuquerque, New Mexico, *An Experimental Study of the Tendency to be Social in the House Sparrow.*

Charles T. Collins, California State University, Long Beach, California, *Development of Temperature Regulation in the House Swift.*

Brian W. Cain, Texas A&M University, College Station, Texas, *Energetics of Growth for Black-bellied Tree Ducks.*

Cynthia Carey and William R. Dawson, University of Michigan, Ann Arbor, Michigan, *Seasonal Adjustment of American Goldfinches to Winter Cold.*

James R. Koplin, Michael W. Callopy and Albert R. Bammann, Humboldt State University, Arcata, California, *Energetics of Wintering Falconiformes: An Empirically-derived and Tested Model.*

Alan H. Brush, University of Connecticut, Storrs, Connecticut, and Dennis M. Power,

Santa Barbara Museum of Natural History, Santa Barbara, California, *House Finch Pigmentation: Carotenoid Metabolism and the Effect of Diet.*

C. R. Blem, Virginia Commonwealth University, Richmond, Virginia, *Geographic Variation in the Body Composition of Starlings.*

Gary D. Schnell, University of Oklahoma, Norman, Oklahoma. *Sexual Dimorphism and Common Factors in Skeletal Measurements of California Gulls.*

Joel Craeraft, University of Illinois at Medical Center, Chicago, Illinois, *Patterns of Size and Shape in Moa Hindlimb Elements: A Multivariate Analysis Approach.*

Jenna Jo Hellack, University of Oklahoma, Norman, Oklahoma, *A Phenetic Analysis of Interspecific Relationships in the Subfamily Cardinalinae.*

Ronald I. Orenstein, University of Michigan, Ann Arbor, Michigan, *Convergence in Stream-adapted Birds.*

Robert L. Paterson, Jr., Central Michigan University, Mt. Pleasant, Michigan, *Factors Influencing Woodcock Habitat Longevity.*

Kathleen E. Franzreb, Arizona State University, Tempe, Arizona, *Variation in the Behavior of Five Avian Species Resulting from Timber Hurvesting in a Mixed-coniferous Forest.*

Sandra E. Jones, 5123 Stansbury Ave., Sherman Oaks, California, *Methods of Coexistence in Insectivorous Mixed Species Flocks.*

Lester L. Short, American Museum of Natural History, New York, New York, *Sympatry Among Thirteen Malayan Woodpeckers—Ecological and Morphological Aspects.*

Howard Levenson, Humboldt State University, Arcata, California, *Time and Activity Budget of a Female Osprey Nesting in Northwestern California.*

Harry W. Power, Syracuse University, Syracuse, New York, *Cost/Benefit Analysis of Mountain Bluebird Foraging Tactics.*

F. Gary Stiles, Universidad de Costa Rica, Ciudad Universitaria, Costa Rica, *Dominance, Territoriality, and Energetics of Some Tropical Hummingbirds.*

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By Jerome A. Jackson, Robert J. Esher, Wayne C. Weber, David F. Werschkul

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This issue of *The Wilson Bulletin* was published on 8 January 1976.

The Wilson Bulletin

Editor Jerome A. Jackson
Department of Zoology
P.O. Drawer Z
Mississippi State University
Mississippi State, MS 39762

Editorial Assistants Robert J. Esher
David F. Werschkul
Wayne C. Weber

Review Editor Robert Raikow
Department of Life Sciences
University of Pittsburgh
Pittsburgh, PA 15213

Color Plate Editor William A. Lunk
865 North Wagner Road
Ann Arbor, MI 48103

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